On meat eating and human evolution: a taphonomic analysis of BK4b (Upper Bed II, Olduvai Gorge, Tanzania), and its bearing on hominin megafaunal consumption

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Abstract:

Recent archaeological work at BK has uncovered abundant taphonomic evidence of megafaunal exploitation by 1.34 Ma hominins. Butchery of small, medium-sized and large carcasses at the site indicate that meat consumption was a crucial adaptive element in the behavior of *Homo erectus*. Current debates on the role played by meat in this early stage of the evolution of the genus *Homo* confront cost signaling interpretations against dietary/physiological interpretations of meat eating and its relation to brain evolution. BBK (including all the archaeological levels) contains the largest amount of hominin-modified bones and butchered animals documented in the Early Pleistocene archaeological record. This evidence supports that meat consumption was tightly linked to the physiology that shaped the evolution of our genus. Hunting was an integral part of the adaptive behavior of *H. erectus* although megafaunal exploitation may have included more opportunistic behaviors. Site organization also suggests that this species may have exhibited a different within-site spatial organization, which differed from previous hominins, as documented at sites such as FLK Zinj. This unveils the need of new behavioral models to explain the functionality of Acheulian central-place sites.

Keywords: *Homo erectus* | megafaunal consumption | Olduvai Gorge | hominin evolution

Article:

1. Introduction

The consumption of megafauna (Bunn's, 1982 carcass size 4 and bigger), particularly the shift from their intermittent to successively more frequent utilization by hominins, is a significant evolutionary event. The earliest evidence for this behavior is a single cut-marked giraffid

metapodial from the site of FLK North at Olduvai Gorge (Domínguez-Rodrigo et al., 2010a) and a small collection of cut-marked megafaunal bones (i.e., hippopotamus) from El Kherba (Sanhouni et al., 2013), both dated to approximately 1.8 Ma, and a handful of cut-marked hippopotamus bones from ~1.5 Ma deposits at Koobi Fora (Bunn, 1994, Bunn, 1997). Leakey's (1971) earlier assertions of elephant butchery at FLK North have been called into question (Domínguez-Rodrigo et al., 2007). The butchery of such large animals appears to have been a sporadic activity, however, and it therefore does not appear that megafauna constituted an important part of the hominin diet prior to 1.5 Ma.

This situation, at least at Olduvai Gorge, changes significantly after middle Bed II times. This is marked by the discovery of butchery marks on the remains of at least one hippopotamus at the 1.5 Ma site of SHK (Domínguez-Rodrigo et al., 2014a). From this moment onwards, the spatial association of stone tools and megafaunal remains becomes more abundant in the gorge's Early Pleistocene archaeological record. This is most spectacularly demonstrated at the Upper Bed II site of BK, where an accumulation of several individuals belonging to *Sivatherium*, *Pelorovis* and *Syncerus*, many with clear traces of hominin manipulation (cut and percussion marks and green breakages), has been uncovered (Monahan, 1996, Egeland and Domínguez-Rodrigo, 2008, Domínguez-Rodrigo et al., 2009a). The frequent exploitation of megafaunal remains over at least three different archaeological levels at BK indicates systematic access to these types of animals and further attests to their importance in the diet of this particular population of hominins by 1.35 Ma. While hippopotamus remains and stone tools are also reported at the Bed IV sites of WK, HEB, and PDK (Leakey, 1994), no taphonomic studies have yet demonstrated their functional relationship. Claims that proboscidean bones at several of these sites were used as tools (Leakey, 1994) have also not been confirmed taphonomically. Several other East African archaeological sites dating to after 1.3 Ma preserve megafaunal remains with evidence of hominin exploitation in the form of cut and percussion marks. For example, localities at Buia (Eritrea) show butchered elements of both large bovids and hippopotamus (one femur, one tibia, and one calcaneum) (Fiori et al., 2004). The exploitation of a giraffid is also documented at PEES4 at Peninj at about 1.3 Ma (Domínguez-Rodrigo et al., 2009b).

Several important questions emerge in this context. Does the exploitation of megafauna, as demonstrated most remarkably at sites such as BK (Fig. 1), signal a major dependence on animal tissues by early Pleistocene hominins, as the evidence for substantial meat-eating at earlier sites such as FLK *Zinj* seems to foreshadow (Domínguez-Rodrigo et al., 2007)? If the ostensible increase after ~1.5 Ma in the frequency of megafaunal acquisition and consumption by hominins in fact reflects an increased reliance on meat, does this indicate that these taxa simply became more readily and easily available across the landscape? Or, perhaps more intriguingly, did bigger hominin group sizes necessitate elevated procurement of the large, high density food packets that megafaunal taxa could provide? Prey size does seem to correlate with group size among some social carnivores (Kruuk, 1972, Gittleman, 1989, Creel and Creel, 1995, Carbone et al., 2007). If meat (and viscerae and bone marrow) consumption was a crucial adaptive element of *Homo erectus*, was it because of its dietary or its cost signaling advantages?

Fig. 1. A, View from the East of the main excavation area at BK. B, insert of the excavation trench into the outcrop where the site is located. C and D, details of the accumulation of nodular and large format artefacts in area B. E, Some of the fossils belonging to *Sivatherium*, including both ossicones, in the process of being consolidated prior to their removal from the ground.

The taphonomic evidence at BK shows that animal tissue, both megafaunal and otherwise, was processed, and presumably consumed, in quantities higher than those previously reported at any other early Pleistocene site. The site is therefore crucial to discussions of the evolution of human subsistence in general and the importance of meat in particular. It has been suggested that meat-eating was a cost signaling product (see summary in Speth, 2010). Therefore, uncovering whether meat was adaptive primarily because of physiological/dietary reasons or because of socio-reproductive reasons is of utmost relevance. Here, we present a preliminary analysis of the faunal assemblage from Level 4b at BK (BK4b) to further address the issues summarized above. In so doing, we hope to refine our understanding of the subsistence behavior of *H. erectus*, a taxon with which very few taphonomically verified anthropogenic faunal assemblages are associated (e.g., Pickering et al., 2004a, Pickering et al., 2004b, Pickering et al., 2008, Egeland and Domínguez-Rodrigo, 2008, Domínguez-Rodrigo et al., 2009a).

2. The BK site: geology and site description

2.1. Archaeological and geological levels

The BK (Bell's Korongo) site is situated on the south wall of the Side Gorge, 3 km upstream from its junction with the Main Gorge. The Side Gorge is only 20 m deep in the BK area and

therefore only the uppermost part of Bed II in addition to small sections of Bed III and Ndutu are exposed (Fig. 2). Stratigraphically, the site's archaeological deposits are located in Bed II just above Tuff IID, which previous work dated to 1.2 Ma (Leakey, 1971) and more recent work places at 1.35 Ma (Domínguez-Rodrigo et al., 2014).

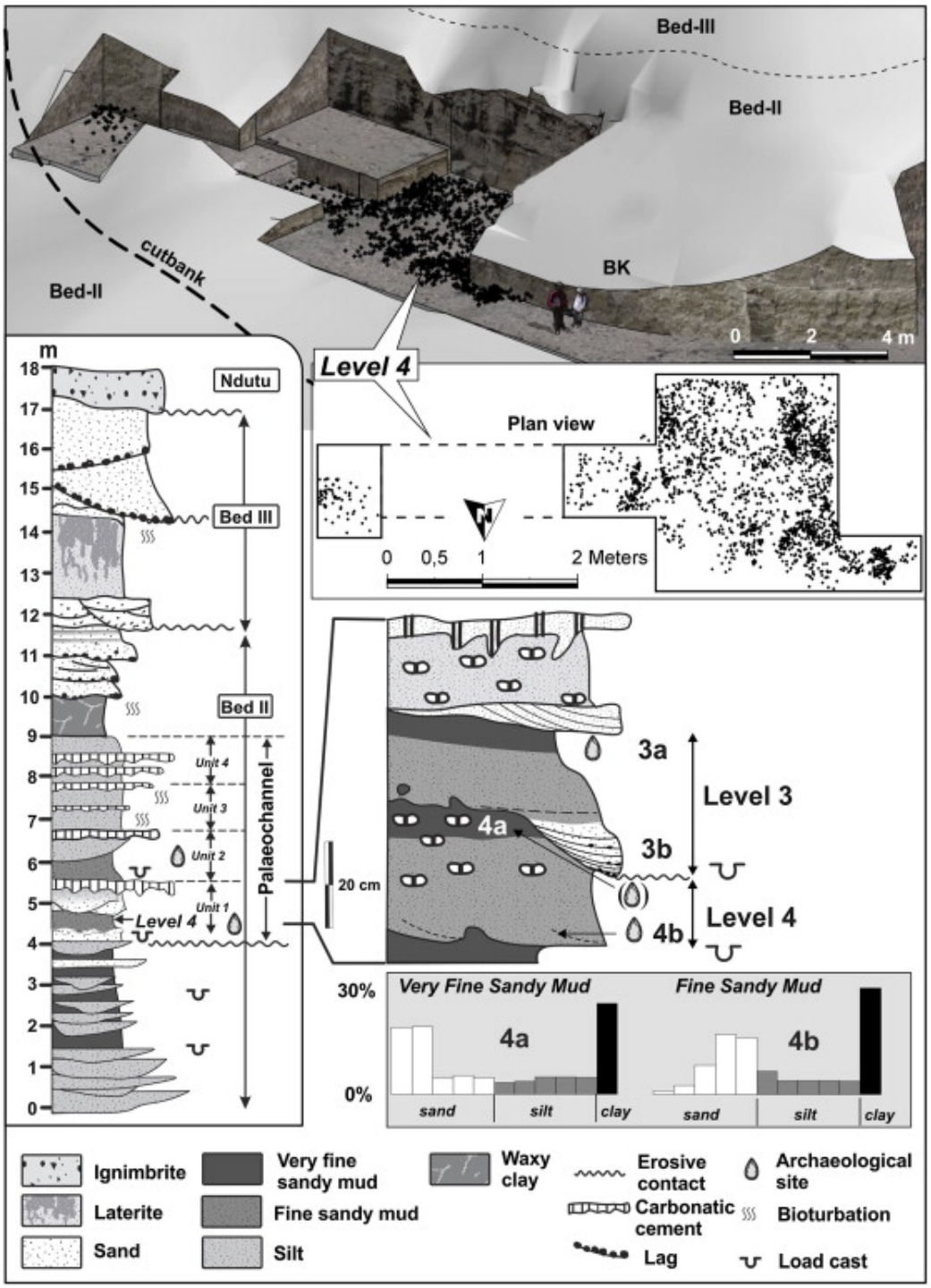

Fig. 2. Location of level 4 at BK and spatial distribution of the archaeological materials (3D and plan view respectively). Stratigraphic section across the Bed II-Bed III and Ndutu units (locality 94) in the Side Gorge (left). Detailed stratigraphic section of levels 3 and 4 (right).

The Bed II outcrops at BK are partially covered by Ndutu sediments and recent colluvial deposits. In this area of the Side Gorge, Bed II is made up of the alluvial and fluvial deposits of a medial to distal fan zone and floodplain facies association. These deposits form lenses of sandy mud bodies with concave bases and concave to flat tops that reflect small, semi-amalgamated channels with very low depth/width ratios. The lenses are up to 30 cm thick, 2–5 m wide, and are floored by channel-lag deposits of very fine gravels to coarse sands and mud clasts. Small isolated clay layers, which are massive, highly bioturbated, and typically less than 20 cm in thickness, are also present. Interbedded among the deposits are small (10–15 cm in thickness), often reworked tuffs cemented with carbonate. Overall, these deposits represent the medium to distal facies of a low energy alluvial system with alternating distributary channels and low energy interchannel areas. The system's sediment supply originated from the eroding slopes of Lemagrut, a volcano located in the Olduvai Basin and directly southeast of BK.

Tuff IID is the most widespread marker in Bed II and is manifest as a reworked, discontinuous, and lithologically variable unit throughout much of the gorge, but can be found relatively well preserved in localities 80 (RHC), 14 (JK), 88 (MNK), 7a (CK) and 40b (MCK) (Hay, 1976). This trachytic tuff is generally 60 cm–150 cm thick, with the lower half commonly laminated and the upper half massive and rootmarked. At BK, Tuff IID lies about 5 m below the top of Bed II and can be followed for hundreds of meters along the right margin of the Side Gorge. In the BK area the tuff is an earthy siliceous, porous, lightweight, and pale yellow (5Y 7/4) tuff between 50 and 70 cm in thickness. It contains a large number of small (~1 mm) siliceous fossil roots.

The BK materials are preserved in low energy fluvial deposits within a wide channel that has eroded the upper part of Bed II, including Tuff IID. The ancient river flowed from south to north and is currently only visible on the paleochannel's right margin. The cutbank shows a minimum depth of 4 m and a width of 50 m, although it appears to be both wider and deeper to the west. The fluvial infill is composed of four sedimentary units that thin upwards and overlap towards the right margin (Fig. 2 lower left). The two lowermost units (Units 1 and 2) are gently undulated, tilt to the west, and increase in thickness towards the left margin of the palaeochannel. These units show a lateral accretion to the west. The overlying units (Units 3 and 4) completely fill the channel basin and spread over the bank. Within the outcrop, a triple facies association (A–C) can be distinguished. Facies association A is only located at the base of the fluvial sequence, over a distinct erosive surface on the underlying alluvial sediments. It represents the channel filling, and contains the coarsest sediment: coarse sand and small gravel (<2 cm), frequently showing cross-stratification and relatively good sorting. Facies association B is composed of lateral accretion units. Each one is 30–50 cm thick and consists of massive silts, very fine sands, and clay. Some of them are floored by channel-lags of coarse sands and low density aggregates of fine gravel-size, composed of clay, silt, and edaphic carbonate (pelletoids). These units tend to erode the previous unit from the west and, in some places, this has affected the archaeological levels. A few lens-shaped bodies, about 40 cm thick and extending laterally for 2–4 m, can be seen interbedded between the sigmoidal units. Finally, facies association C represents the floodplain processes. They are composed of upward thinning layers of silty clay. Calcium carbonate cements are developed on top of each layer. Such post sedimentary features point to incipient soil development during phases of subaerial exposure. Carbonate distribution

increases vertically within the sequence, which suggests a progressive reduction in flood frequency. Cemented carbonate is the most usual type, but hard-pans and calcretes are also present, indicating other complex postdepositional and edaphic processes. Archaeological levels 3 and 4 occur in sedimentary Unit 1 within facies association B.

Domínguez-Rodrigo et al. (2009a) previously differentiated four archaeological levels at the site. One of them, level 3 (BK3) was correlated to the exposed and richly fossiliferous level of Leakey's (1971) exhibit trench. Level 3 in the first trench excavated by TOPPP (The Olduvai Paleoanthropology and Paleoecology Project), just adjacent to the Leakey trench, contained considerably fewer fossils, probably due to erosion. The underlying level 4 (BK4), which at the time was only just exposed, contained a promising concentration of megafaunal remains in association with heavy duty stone tools. This contrasted with the overlying levels, which were dominated by stone tools made in small formats (Diez-Martín et al., 2009). Subsequent fieldwork between 2009 and 2012 exposed a substantially larger area and a deeper sequence, which has enabled a more detailed reconstruction of the dynamics of fluvial erosion and sedimentation within the laterally variable stratigraphy and the discovery of additional archaeological levels.

The material of BK3 was found within the sandy matrix of a shallow channel. Level 3 is a 30 cm thick fining upward irregular layer. Bedload is muddy coarse sand, composed of very coarse sand (19%), coarse sand (19%), medium to very fine sand (14%), silt (26%) and clay (25%). Most of the clay forms small alluvial aggregates (clay pellets and pelletoids), which show a low density bedload. They show parallel and cross-bed lamination, and mud clasts and bone fragments are also frequent. Locally, such bedload generates cut and fill shapes, small erosive channels and scours over the 4a layer. The second half of the upper part of Level 3 ends with very fine sediment, which corresponds to the low flow velocity stage. BK3 was underlain locally by a silty sand layer, which itself rested on top of another shallow channel (level 3a, BK3a), which locally overlied another similar sequence of sandy silt and another shallow channel (level 3b, BK3b). This latter channel tilted towards the lowest part of a point bar and it eroded part of the underlying clay deposit containing level 4. These alternating alluvial layers contain fossils that show no clear sedimentary hiatus. These levels probably represent multiple depositional events, as skeletal remains representing the deposition of a single carcass sometimes span several geological layers. For instance, a partial elephant carcass represented by the axial skeleton (vertebrae and ribs) was deposited on BK3a, but the fossils, due to their size, extend into the overlying BK3 sediments. A handful of elephant rib fragments were also found in BK3b, although given the large number of megafaunal individuals accumulated at the site it cannot be ruled out that they belong to a different carcass.

Level 4 is located within a clay layer and the archaeological material seems to be vertically concentrated in two positions: at the top of the clay layer with some vertical dispersion (BK4a) and the lower part of the clay deposit (BK4b). A vertical hiatus between the fossils of BK3b and BK4b exists over a large part of the excavated area, a situation that occurs even when the top of the clay layer is eroded (Domínguez-Rodrigo et al., 2009a). This, together with the easily outlined clay layer of BK4b, confirms the identification of BK4b as a separate level. Given that the channel overlying the level 4 clay erodes the underlying deposit, some materials from the top of the clay may have been reworked and even mixed with materials from BK3b, especially on the western side of the excavation. Thus, we exclude the BK4a materials, which fortunately are

not abundant, from the present analysis. Because a majority of fossils and stone tools from level 4 were found in the lower half of the clay layer (BK4b), this material forms the focus of the present work. It is also, along with BK1 and BK2, the best evidence for a horizontally discrete use of the space by hominins at the site.

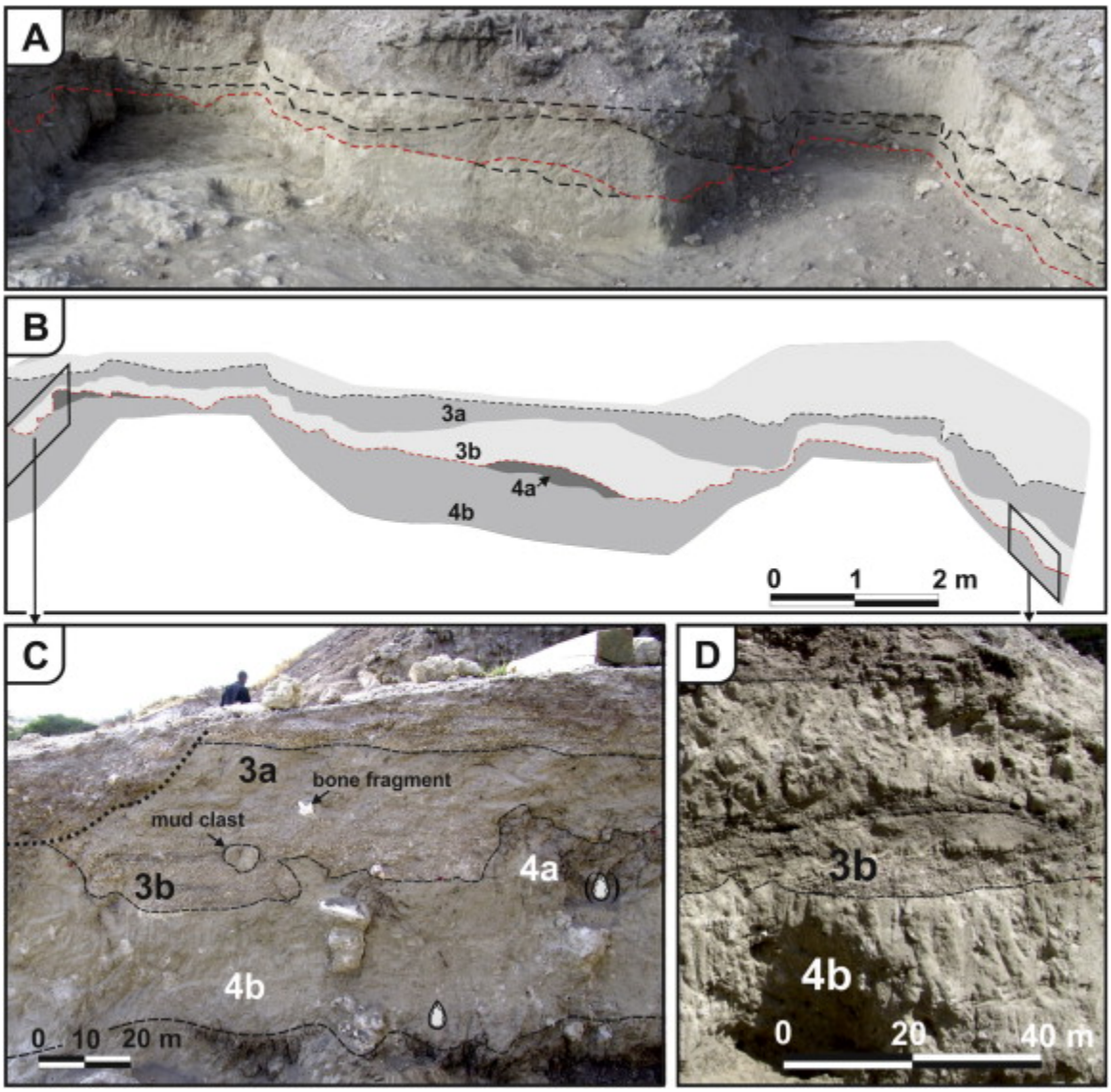

Fig. 3. A, panoramic view of levels 3 and 4 at BK. B, stratigraphic interpretation of the site. C and D, close-up views of contacts between levels 3 and 4.

Level 4 shows a variable thickness of 20–30 cm, although in some places it reaches 40 cm in thickness, and it is gently wavy and tilted 2–4° to the NW. The base is also irregular due to load deformation (load cast). It is massive, although some fining upwards can be distinguished. Very locally, Level 4 is floored with a low density bed-load (<5 mm)-carbonate aggregates, mud-clasts and little coarse sand- that infill a small scale and non-continuous depressions of less than 2–3 cm thick. They correspond to the initial flood stage but neither erosional nor current structures (marks, ripples, cross stratification, etc.) have been identified, showing a low velocity sedimentation process. In most of the outcrop, Level 4 is massive and composed of clay (33%),

silt (22%), very fine and fine sand (33%) and medium sand (12%) (fine sandy mud). The largest concentration of artefacts and bones spread along the base (BK4b). The top of Level 4 (4a) is partially preserved due to the overlying Level 3, which is highly erosive (Fig. 3). Level 4a is 5–10 cm thick and consists of clay (38%), silt (35%), very fine sand (14%) and fine sand (9%) (very fine sandy mud), which corresponds to the lowest flow velocity stage (decantation).

Level 4 (ranging between 30 and 40 cm of depth) is, therefore, understood more as a geological level than a strictly archaeological one since it may be part of a broader archaeological deposit. A 1 m^2 test pit exposed a sandy layer after the removal of the clay filled with archaeological materials. The only difference in the archaeological sequence is a change in lithology and, thus, of depositional environment. However, given the moderately discrete nature of BK4b, further work will be needed to reveal if the fossil evidence exposed in such a small test pit can be documented in the remainder of the area excavated. The present work is thus preliminary until further excavation is undertaken and the sequence under BK4b is fully exposed.

The intense butchering activities documented at BK (with deposition of materials over 2 m of sedimentary sequence) shows that the deposit underlying BK2 contains limited integrity (number of agents responsible) and resolution (number of depositional events). However, BK4b provides a higher resolution in comparison, which enabled the discovery of several hominin activities through the horizontal distribution of materials on the BK4b paleosurface. Although this level was previously identified as the *Pelorovis* level described by Leakey, 1971, Domínguez-Rodrigo et al., 2009a lateral expansion test trenching towards the western corner where the excavations from the 1950s exposed a MNI of 24 Pelorovis showed that on that area, the thick clay deposit that contained the megafaunal remains is stratigraphically situated under BK4.

The moderately discrete nature of BK4b is revealed first by its dense concentration of fossils and stone tools at the lower half of the clay deposit, compared to the substantially less dense upper part and, second, by several taphonomic considerations. One is the discovery of a partial carcass of a *Sivatherium* in most of the area exposed through excavation, comprising elements from the cranial, axial and appendicular skeleton. Another argument is the discovery of more than a dozen hominin remains on the BK4b paleosurface attesting to its discrete vertical distribution (Domínguez-Rodrigo et al., 2014b). Taphonomic processes are detected horizontally at BK4b, which was formed under low to moderate energy sedimentary conditions. The taphonomic study of this site provides compelling evidence for the exploitation of large quantities of meat by early Pleistocene hominins and calls for interpretations that elaborate on the role that meat eating played in the survival of those ancestors.

2.2. The BK excavated area

A total of 46 m^2 of BK4b have been exposed thus far (Fig. 4). Fig. 5 shows the intimate spatial association of stone tools and fossils, the former concentrated in higher densities in the western half of the trench. The lithic concentration is highlighted in Figs. 5 and 6. Fig. 7 shows a curious circular cluster of materials. It was near this cluster that a hominin radius was found (Domínguez-Rodrigo et al., 2014b). The excavation indicates that the archaeological level extends well beyond the exposed areas and that it continues to the west (down the point bar)

towards the river channel. Future work will seek to connect the west corridor of the excavation with the area exposed in the 1950s (Leakey, 1971).

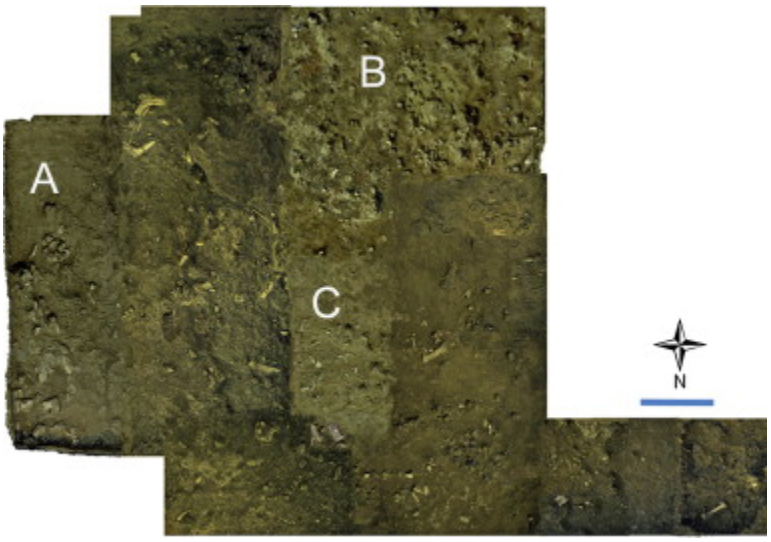

Fig. 4. Surface of BK4b showing fossils and stone tools. Three areas are highlighted: A, carbonated concentration of fossils from macromammals; B, concentration of fossils and stone tools, highlighted because of the density of nodular pieces; C, circular arrangement of fossils and tools. These three areas can be seen in more detail in Figs. 6 and 7 and have been reconstructed in interactive 3D via fotogrammetry and can be seen in Supplementary Online Information. Scale = 1 m.

The excavation was conducted with small hand tools during the removal of sediments in the fossiliferous level. Sediments were completely sieved and every single fragment collected. Fragments over 2 cm were plotted with the aid of a laser total station. Unfortunately, some specimens larger than 2 cm could not be plotted in situ, as heavy carbonation required their complete exposure to take place afterwards during laboratory work. Sediment compaction affected many of the fossils, with cracks and diagenetic breakage planes resulting in the fragmentation of specimens as they were removed from the soil (see Fig. 8). When possible, specimens in danger of fracture during excavation were stabilized prior to removal (Fig. 1c) to prevent excessive in situ fragmentation or were repaired in the laboratory.

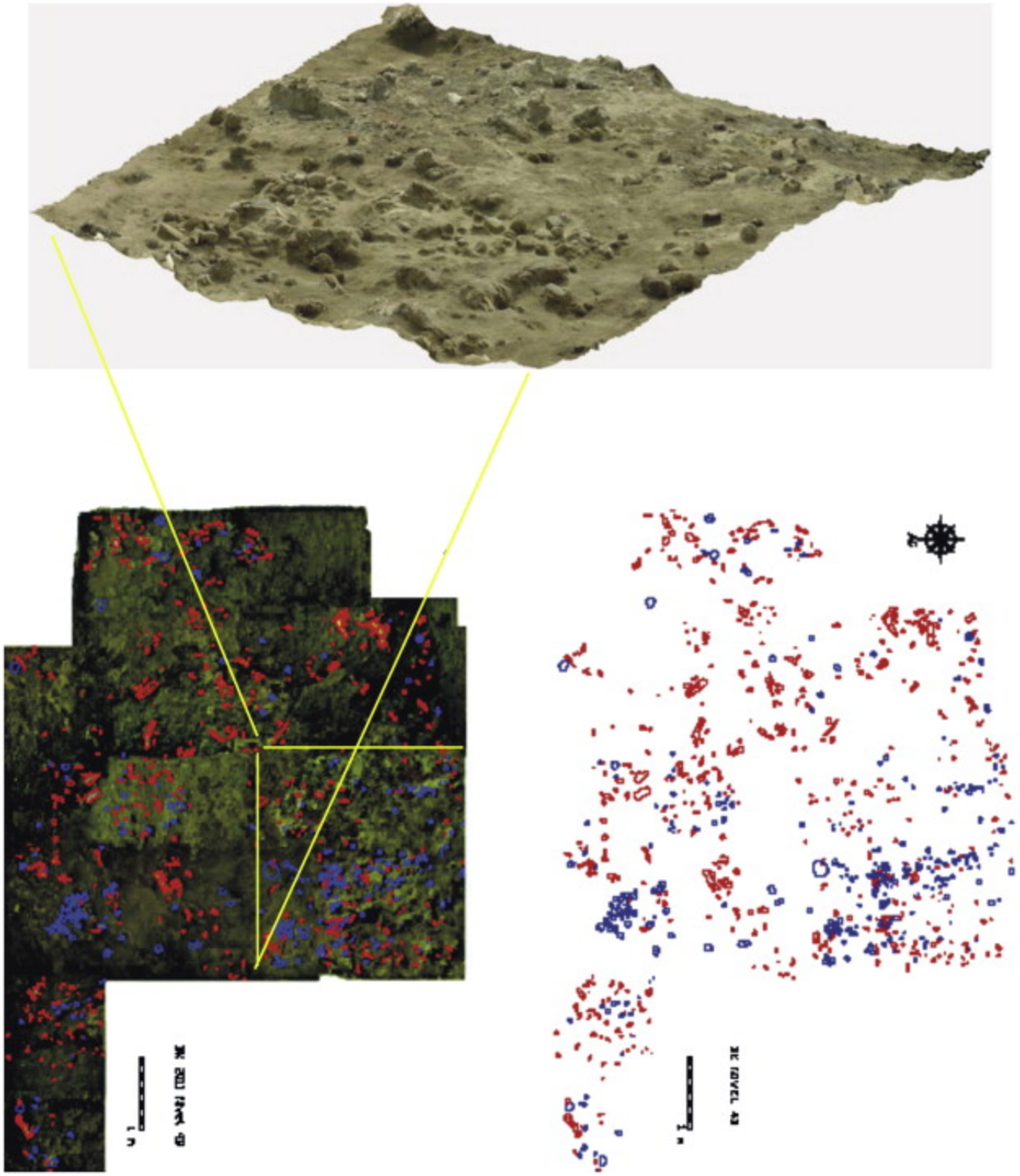

Fig. 5. Lower right part, map of distribution of artifacts (in blue) and fossils (in red) on BK4b, overlaid to the photographic reconstruction of the paleosurface (lower left part). Upper image shows an area (B in Fig. 4) where there is a high concentration of nodular artefacts, reconstructed with photogrammetry techniques.

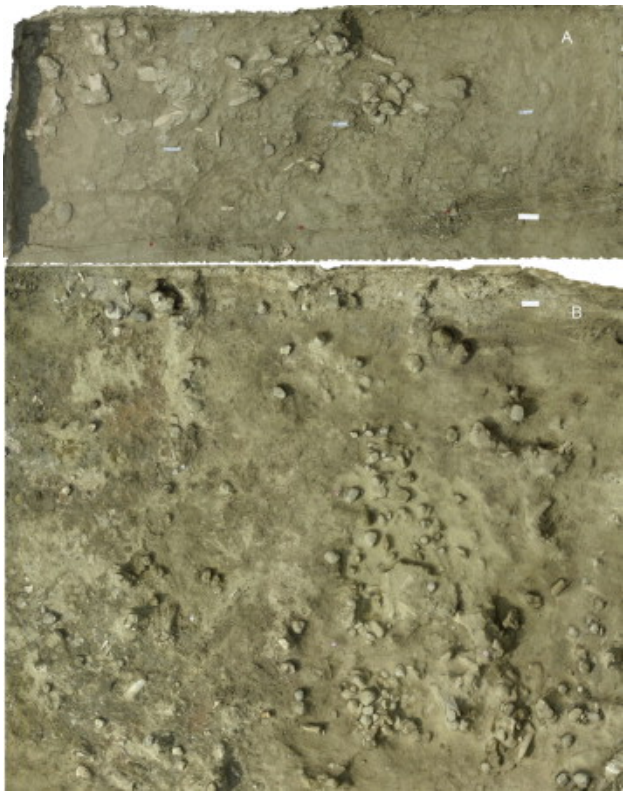

Fig. 6. Areas A (A) and B (B) from the BK4b paleosurface, as highlighted in Fig. 4. These areas have been reconstructed in 3D via fotogrammetry and can be seen in Supplementary Online Information. Scale = 10 cm.

Fig. 7. Area C (C) from the BK4b paleosurface, as highlighted in Fig. 4. Notice the circular cluster of fossils and stone tools surrounded by a largely devoid space. This area has been reconstructed in 3D via fotogrammetry and can be seen in Supplementary Online Information. Scale = 10 cm.

Fig. 8. Example of a large megafaunal long bone shaft with a spiral green fracture, embedded in a carbonate matrix, showing several cracks, prior to its removal from the ground.

3. Methods and samples

3.1. Orientation analysis

Three-dimensional spatial information for plotted archaeological items was collected with total stations. Total stations have also been used to document the projection of the axis of each object (e.g., McPherron, 2005). However, we preferred not to use this protocol, since the orientation of each item must be derived graphically after plotting all the information. Therefore, vertical and horizontal orientation was collected directly from each item to the nearest degree prior to removal with the aid of compasses and clinometers (Voorhies, 1969, Fiorillo, 1991, Alcalá, 1994, Howard, 2007). These measurements were taken along an A-axis that divided the item more or less symmetrically along its longitudinal axis. This symmetry axis has been shown to be taphonomically informative, as experiments show that long objects tend to orient according to their longitudinal axes (Toots, 1965, Voorhies, 1969). Orientation measurements were taken on all items, regardless of size, that showed a well-defined longitudinal axis (i.e., specimens that are at least twice as long as they are wide).

Orientation data were displayed graphically using rose diagrams (Rockworks 15.0 software) and stereograms (OpenStereo software). Statistical treatment was conducted using the R software package (http://www.r-project.org). Isotropy (or randomness in orientation) was statistically assessed using omnibus tests, which can detect any trend towards non-uniformity. A Kuiper's test (V) was used for this purpose. However, general omnibus tests are not very effective in detecting unimodal orientations. To test uniform distributions against unimodal distributions, Rayleigh's (R) test was applied (Fisher, 1995). This test is very efficient in detecting unimodal patterns in a sample of vectors or bipolar patterns in axes prior to their conversion in vectors (Fisher, 1995). A model for assessing the normal distribution of circular data is the von Mises distribution. For this distribution, the dispersion is quantified by a concentration parameter k, with a $k = 0$

corresponding to an isotropic distribution and increasing values with a trend towards anisotropy. The Watson (U^2) test is a goodness-of-fit statistic for the von Mises distribution. Values with $p = >0.05$ indicate that the null hypothesis of isotropy cannot be rejected. The three tests were applied in the present study and the R functions used were “rayleigh.test”, “kuiper.test” and “watson.test” from the R “circular” library.

It is often desirable to supplement tests with graphical procedures (Fisher, 1995). For this purpose, Woodcock's diagrams where linear, planar, and isotropic fabrics can be displayed were also used (Woodcock, 1977, Lenoble and Bertran, 2004). For comparative purposes, the small (<5 cm) and intermediate (5–10 cm) sized specimens with clearly-defined A-axes were plotted separately in the stereogram to detect size-dependent orientations. Because sample sizes were relatively small, size-dependent samples were bootstrapped 500 times each (with replacement).

3.2. Faunal analysis

We employed a number of methods to reconstruct site formation processes, assess site integrity, and evaluate the contributions of various biogenic agents to the faunal assemblage. Since water jumbles tend to produce faunal assemblages biased toward larger fragments, we recorded maximum length of each fragment and examined the distribution of fragment lengths to detect possible size-sorting, which would be indicative of preservation bias. This was done at three levels. First, size-sorting was examined among *all* fragments. At the second level, only long bone fragments were considered, as cancellous axial bones undergo different fragmentation patterns than do denser limb bones (Domínguez-Rodrigo and Martínez-Navarro, 2012). At the third level, only those long bone fragments displaying green breakage were considered. This distinction is made because diagenetic (dry) breakage is relatively common in the assemblage and thus the specimen size distribution in the recovered assemblage may be quite distinct from that of the original deposited assemblage. Signs of polishing or abrasion were recorded as a final appraisal of fluvial activities within the site. Polishing or abrasion may be found in both transported assemblages and non-transported assemblages exposed to moving water and sediments, such as those found in sand strata (Thompson et al., 2011).

Some specimens were not included in the present study because they are currently undergoing restoration, most frequently due to the adhering carbonate matrix that covers them. All appendicular (including limb shaft) and axial specimens were identified to element whenever possible. Skeletal part profiles were analyzed by dividing the carcass into anatomical regions: skull (horn, cranium, mandible and teeth), axial (vertebrae, ribs, pelves, and scapulae) and appendicular (limb bones), with limbs further divided into upper (humeri and femora), intermediate (radii and tibiae), and lower (metapodials) units (Domínguez-Rodrigo, 1997). Pelves and scapulae are often classified separately, but we decided to lump these together with vertebrae and ribs, given their overall similarity in bone texture and taphonomic properties (these elements are mostly cancellous and fragile). This has a particularly important effect when working with highly fragmented assemblages (see Domínguez-Rodrigo et al., 2007). These profiles are based on the number of identified specimens (NISP) and an estimate of the minimum number of elements (MNE). Specimens were also identified, when possible, to carcass size: small carcasses include Bunn's (1982) sizes 1 and 2, medium-sized carcasses are Bunn's size 3 and large carcasses are sizes 4 to 6.

It has been shown that epiphysis-based and shaft-based limb bone MNE estimates at Olduvai can differ substantially (Domínguez-Rodrigo et al., 2007). In estimating MNEs, some researchers employ a geographic information system (GIS), treating the bone as a "landscape" to determine overlapping fragments (Marean et al., 2001). While this approach has merit, particularly when working with extremely large assemblages, more confidence is attained when overlap is documented manually. We therefore employ an integrative approach, as outlined by Yravedra and Domínguez-Rodrigo (2009), that is built on the bone section methods of Patou-Mathis, 1984, Patou-Mathis, 1985, Münzel, 1988, and Delpeche and Villa (1993). Following Delpeche and Villa (1993) and Münzel (1988), shafts were divided into equally-sized sectors (upper, mid, and lower), irrespective of muscle insertion sites. These sectors are easily differentiated, and can be oriented as cranial, caudal, lateral, or medial (see Yravedra and Domínguez-Rodrigo, 2009 for a description of the criteria used to define each shaft sector). Additional identification criteria include cortical bone thickness, cross-sectional shape, and properties of the medullary surface (Barba and Domínguez-Rodrigo, 2005). MNEs were then estimated by laying specimens out on a flat surface and organizing them according to element and size group. In the process, criteria used in a comprehensive analysis (Lyman, 1994) such as element size, side, age, and biometrics, could be easily observed in side-by-side comparisons.

It has been argued that density-mediated biases in skeletal part profiles can be partially overcome if the frequency of appendicular bones can be accurately estimated (Marean and Cleghorn, 2003, Cleghorn and Marean, 2004, Marean et al., 2004). This is because while no taphonomic analysis can currently evaluate the degree of destruction for those skeletal elements that are least likely to survive (e.g., axial bones), the proper identification and quantification of those elements most likely to survive due to their high density (limb shafts, selected skull sections, teeth) can lead to better estimates of carcass representation prior to the various taphonomic processes that may have occurred in any given site as well as a better understanding of these processes (Marean and Frey, 1997; Marean and Kim, 1998; Marean, 1998, Costamagno, 2002, Pickering et al., 2003, Marean et al., 2004).

Faith and Gordon (2007) argue that skeletal element representation can be quantified using the Shannon evenness index. Basing their argument on optimal foraging theory, they note that foragers' choices in terms of transporting carcass parts will be reflected in the evenness of the distribution of specimens across classes of high-survival elements (*sensu* Marean and Cleghorn, 2003, Cleghorn and Marean, 2004). Axial elements, as noted earlier, are comparatively low-density and thus are more vulnerable to destruction, whereas crania and appendicular elements are more likely to survive and can be informative about foragers' transport and butchery decisions (Marean and Cleghorn, 2003). When entire carcasses have been transported, or where no transport has occurred at all, high-survival elements should be evenly distributed (standardized by their frequency in the vertebrate body). As transport becomes increasingly selective, favored elements become overrepresented and evenness declines. If transport decisions are at least partially mediated by transport distance, then an even representation of cranial and long limb bones (unselective transport) would indicate short-distance carcass transport whereas uneven representation (selective transport) implies long-distance transport. Shannon's evenness index was obtained following Faith and Gordon (2007), where evenness = $\mathbf{\Sigma} - p_i/\ln \mathbf{S}$ and **S** is the number of elements and p_i is the standard proportion of specimens for the *i*th element. This

index was applied to long limb bones, skulls, and mandibles and was analyzed separately by carcass size group.

As noted earlier, it became clear during excavation that sediment compaction had affected the faunal assemblage. Several bones showed cracks and diagenetic breakage planes that caused further fragmentation as specimens were excavated. Identification of breakage planes as green or dry (including diagenetic) was carried out following Villa and Mahieu (1991): dry breakage planes tend to be longitudinal and/or transverse to the long axis of the bone, possess a nearly 90° angle between the cortical and medullary surfaces, and show an uneven breakage plane surface with micro-step fractures and a rough texture. Green breakage planes have smoother surfaces and are more likely to be oriented obliquely to the long axis of the bone. Breakage pattern analysis followed methods outlined by Domínguez-Rodrigo et al. (2007).

Although notches, which are semi-circular outlines along otherwise rectilinear fracture edges associated with a medullary flake scar, often form an integral part of fracture analysis, the lack of a suitable experimental framework for interpreting their frequencies and form on medium and large carcasses (Capaldo and Blumenschine, 1994, De Juana and Domínguez-Rodrigo, 2011) precludes their detailed consideration in this study.

A detailed analysis of bone surface modifications was also carried out. Cortical surfaces were first evaluated for preservation; that is, the likelihood that surface modifications, if present, would be visible and confidently identified. Several classes of surface mark were identified, including cut marks, tooth marks, percussion marks, and natural marks caused by biochemical reactions and/or abrasion. Cortical surfaces were examined with hand lenses under strong direct light following the methods and diagnostic criteria of Blumenschine, 1988, Blumenschine, 1995 and Blumenschine and Selvaggio, 1988, Blumenschine and Selvaggio, 1991 for tooth and percussion marks and Bunn (1981) and Domínguez-Rodrigo et al. (2009a) for cut marks. Mark frequencies are calculated as both raw estimates and, following Pickering et al. (2008), corrected estimates. The latter measure attempts to correct for both the inflation of specimens through dry breakage and artificial reduction of mark frequencies when specimens with poor cortical preservation are compared to well-preserved specimens. Pickering et al. (2008) suggest recalculating the original number of specimens by (1) dividing the number of specimens with dry breakage by two (as each specimen will break into at least two fragments), (2) calculating the number of specimens with poor cortical preservation, and (3) combining these two values and subtracting them from the total number of specimens. This enables a more realistic comparison of archaeological data with modern experimental assemblages that have not undergone any diagenetic bone breakage or differential bone surface preservation.

Tooth and percussion mark frequencies were tallied by the epiphyseal and midshaft parts of long limb bones of Blumenschine (1988). Near-epiphyseal parts were not included in analyses because of problems with the way this part is defined and thus how marks are counted (Domínguez-Rodrigo and Barba, 2006). For example, a 10 cm shaft specimen that preserves one cm of trabecular tissue on its medullary surface would, according to Blumenschine's (1988) scheme, be classified as a near-epiphyseal part, this despite the fact that marks may actually occur on the midshaft that makes up 90% of the specimen. The identification of epiphyseal and midshaft specimens, on the other hand, is straightforward, so marks on these parts are presented

for comparison to published experiments. Cut marks were tallied by element and section following Domínguez-Rodrigo (1997). Given the frequent occurrence of sediment abrasion among the BK4b fauna, the cut mark estimates presented here are conservative and follow the protocols of Domínguez-Rodrigo et al. (2009a).

Conflicting interpretations of surface modifications and their repercussions for hominin and carnivore access to carcasses still persist (e.g., Pante et al., 2012). This, we feel, is largely due to the fact that some scholars (e.g., Selvaggio, 1994, Selvaggio, 1998a, Selvaggio, 1998b, Blumenschine, 1995, Capaldo, 1997, Capaldo, 1998) do not interpret cut marks, percussion marks, and tooth marks within an integrated framework and thus fall victim to serious contradictions. The joint observation of all three mark classes within an experimental context can help to overcome this, and here we simultaneously analyze all bone surface modifications from BK4b in reference to a Felid–Hominin model (F–H), a Felid–Hominin–Hyenid (F–H–H) model, and a Hominin–Carnivore (H–C) model (see Domínguez-Rodrigo et al., 2014c). Due to the small number of cut-marked bones from small carcasses (n = 3) and the lack of proper reference data for felid consumption of small animals, only medium-sized and large carcass data were compared to these experimental frameworks.

Multiple discriminant analysis (MDA) was used to differentiate among distinct experimental groups and to classify the BK data accordingly. This type of statistical analysis was selected because whereas principal component analysis (PCA) maximizes sample variance, MDA maximizes intergroup variance and thus more readily enables factor discrimination. Mixture discriminant analysis (MXDA) was utilized because it permits the use of non-normal distributions and heteroscedastic samples (Hastie and Tibshirani, 1996, Ma and He, 2008). Prior to MXDA, surface mark data were bootstrapped, which provides superior estimates of parameters when sample sizes are small. Hall's (1992) uniform resampling procedure argues for a step-wise approach to bootstrapping, whereby a small number of replications are run and continued until error bias stabilizes. We followed this approach and obtained error bias stabilization before reaching 1000 replications.

3.3. Spatial and geostatistical analysis

Spatial point pattern analysis was performed by applying Complete Spatial Randomness tests (Bivand et al., 2009). These tests analyze if points are independently and randomly distributed over any given area or if they are distributed in clustered and/or patterned ways. To test for patterned distributions, the G (Gest) function was used, which measures the distribution of distances from arbitrary points to the nearest point (“nearest event”). The compatibility of complete spatial randomness with the point pattern is evaluated by plotting the observed function G against the theoretical expectation. The latter is simulated by multiple pair-wise estimations, which create envelopes or confidence intervals for expected complete spatial randomness, which can then be used to assess if the observed function is contained inside (Bivand et al., 2009). These envelopes are computed by randomly simulating a number of point patterns so that the summary function is computed for all of them jointly (using Monte Carlo computation methods). Spatial distributions of specimens associated with specific taphonomic variables (e.g., bone preservation, chemical modification of cortical surfaces, polishing and abrasion) were carried out using the “sp” library in R. Variograms, which model spatial correlations between distance and

any specific variable, offer a good indication of anisotropy in this context. For example, in the present study a variogram was used to assess whether specimen size distribution is spatially random. Anisotropy was measured using a range ellipse with four main directions (0°, 45°, 90° and 135°). The analysis was carried out using the "geoR" and "gstat" R libraries (Bivand et al., 2009). For specimen size distribution, class boundaries were assigned with the Fisher–Jenks natural break method (Bivand et al., 2009) by using the "classInt" R library.

4. Results

4.1. Orientation analysis

A stereographic projection of bones with a clear A-axis shows a uniform distribution, with most showing only slight plunge and no horizontal trend (Fig. 9a). The mean direction is about 18°North–198°South as shown by the 95% confidence interval of the stereogram, but, as the rose diagram shows (Fig. 9b), most of the azimuth confidence interval shows no clearly identifiable anisotropic orientation. The Woodcock diagram shows an isotropic fabric for the assemblage, with a von Mises distribution k concentration value under 0.2 ($k = 0.02$) (Fig. 9c).

Statistical tests show that the null hypothesis of uniform distribution cannot be rejected. This is supported by a Rayleigh test of a general unimodal alternative ($R = 0.113$, $p = 0.893$), a Kuiper test of uniformity ($V = 1.329$, p=>0.15), and a Watson goodness-of-fit test of circular uniformity ($U^2 = 0.06$, p = >010). Together, these suggest that the assemblage is largely autochthonous and that post-depositional disturbance by hydraulic flows was not sufficiently strong to preferentially orient materials in the archaeological deposit. Stereographic projections of small and intermediate-sized specimens separately (both sub-samples were bootstrapped) show that no size-dependent orientation can be detected (Fig. 9d,e).

When orientation is measured according to alternative A-axes, such as D or MBR axes, as suggested by de la Torre and Benito-Calvo (2013), no anisotropy is detected either. This is documented when using an elongation index 1.6 or, more appropriately, elongation index 2.0 (length is twice the size of breadth) (see Supplementary Information and figures).

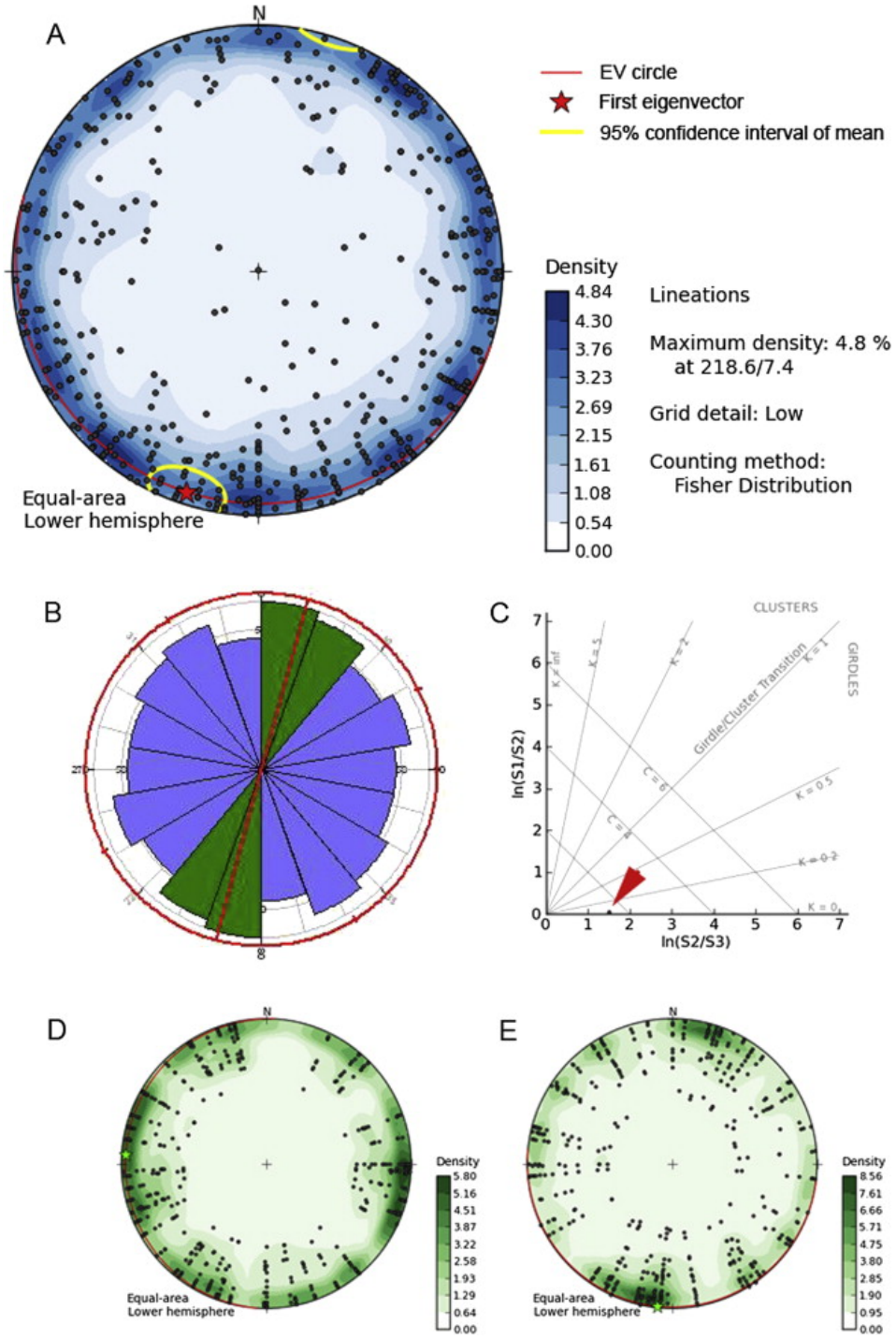

Fig. 9. A, Stereogram showing the azimuth orientation of all the specimens with a longitudinal axis at BK4b. The first eigenvalue comprising most of the inertia is shown, as well as the confidence interval of the mean trend/plunge orientation (in yellow). B, rose diagram showing uniform bone orientation. C, Woodcock diagram shows an isotropic fabric for the assemblage, with von Misses distribution k concentration values under 0.2. D, Stereogram showing the azimuth orientation of the bootstrapped sample (n = 500) of small specimens (<5 cm) with longitudinal axis. E, Stereogram showing the azimuth orientation of the bootstrapped sample (n = 500) of intermediate-sized (5–10 cm) specimens with longitudinal axis.

4.2. Faunal analysis

4.2.1. Skeletal part profiles

Table 1. Minimum number of individuals (MNI) found at BK4b.

	MNI
Bovidae	
Antidorcas recki	2
Kobus cf. kob	1
Tragelaphus sp.	1
Taurotragus oryx	1
Alcelaphini size 3a	2
Connochatetes taurinus	2
Megalotragus sp.	1
Syncerus acoelotus	1
Pelorovis oldowayensis	2
Suidae	
Kopochoerus olduvaiensis	3
Metriochoerus compactus	4
Equidae	
Hipparion cornelianum	1
Hipparion sp.	1
Equus oldowayensis	3
Hippopotamidae	
Hippopotamus sp.	2
Rhinocerotidae	
Ceratotherium sp.	1
Elephantidae	
Elephas sp.	1
Giraffidae	
Sivatherium sp.	2
Cercopithecidae	
Theropithecus sp.	1
Hominidae	
Paranthropus boisei	1
Felidae	
Panthera cf. leo	1
Hystricidae	
Hystrix sp.	1
Total	35

The BK4b bone assemblage is composed of 1156 specimens representing a large array of taxa and, if one considers cranial and post-cranial elements, at least 35 individuals (Table 1). Of these fragments, only 870 specimens could be attributed to carcass size (Table 2, Table 3, Table 4). Large carcasses (NISP = 412) are better represented than medium-sized (NISP = 379) or small (NISP = 79) carcasses. Small animals are mainly represented by dense elements or bone parts (Table 2). Cancellous bone, such as axial elements (ribs and vertebrae), compact bones (carpals,

tarsals, and phalanges), and long bone epiphyses are underrepresented as measured by MNE and MNI. Proximal epiphyses from humeri or tibiae and both epiphyses from radio-ulnae are almost absent, and ribs and vertebrae are virtually non existent among small carcasses.

Although specimens from medium-sized carcasses are almost four times as abundant as those of small carcasses, a similar pattern of skeletal abundance exists regardless of taxa (Table 3). With the exception of ribs, which are relatively abundant (NISP = 48; MNE = 12), the axial skeleton is generally underrepresented, as are compact bones. Long bones are most frequently represented by shaft fragments, and the least dense epiphyseal ends (proximal humerus, distal radius, proximal tibia) are almost completely absent. Teeth, as the densest elements, are the best represented anatomical part although, given the MNI documented, a large part of them are also missing.

Large carcasses show a more even, though still incomplete, anatomical representation (Table 4). Most long bone epiphyses are represented, although still less so than shafts. Relative to MNI, compact bones are also more abundant than among other carcass sizes. Nevertheless, the least dense epiphyseal parts (proximal humerus, distal femur, proximal tibia, distal radius) are still less frequently represented than their opposite parts. The axial skeleton is better represented than it is among smaller carcasses, but a large part of it is also missing relative to the number of individuals.

Table 2. Skeletal part profiles of small carcasses at BK4b. NISP, number of identified specimens; TM, tooth marked specimens; PM, hammerstone-percussed specimens; CM, cut marked specimens; MNE, Minimum number of elements.

	NISP	TM	PM	CM	NISP with good preservation	MNE
Horn	5				5	1
Skull	3				1	1
Mandible	1				1	1
Teeth	5				5	
Vertebrae	2					2
Ribs	8	1		1	5	4
Scapulae	1					
Pelves	1				1	
Humerus						2
Prox. epi.						
Shaft	3				1	
Dist. epi.	2	1			1	
Radius–ulna						1
Prox. epi.						
Shaft	1		1		1	
Dist. epi.						
Metacarpal						2
Prox. epi.						
Shaft	3			1	3	
Dist. epi.	3					
Femur						1
Prox. epi.	2				2	
Shaft	1					

	NISP	TM	PM	CM	NISP with good preservation	MNE
Dist. epi.	1					
Tibia						1
Prox. epi.						
Shaft	7		1		4	
Dist. epi.	1				1	
Metatarsal						1
Prox. epi.						
Shaft	9	2			4	
Dist. epi.						
Carpal/tarsal	3				2	3
Phalanges	2				1	2
Other						
Indeterminate	15			1	3	
Total	79	4	2	3	41	22

Table 3. Skeletal part profiles of medium-sized (size 3a,3b) carcasses at BK4b. NISP, number of identified specimens; TM, tooth marked specimens; PM, hammerstone-percussed specimens; CM, cut marked specimens; MNE, Minimum number of elements.

	NISP	TM	PM	CM	NISP with good preservation	MNE
Horn	5				5	4
Skull	8				7	3
Mandible	7	1	3		4	3
Teeth	84				84	
Vertebrae	16			2	9	16
Ribs	48	1		2	18	12
Scapulae	7	2		3	4	5
Pelves	8	2			6	
Humerus						7
Prox. epi.						
Shaft	30	2	2	2	13	
Dist. epi.	5				4	
Radius–ulna						4
Prox. epi.	1			1	1	
Shaft	8		2		6	
Dist. epi.						
Metacarpal						5
Prox. epi.	3					
Shaft	8				2	
Dist. epi.	2				2	
Complete	1	1				
Femur						4
Prox. epi.	1				1	
Shaft	10	1	3	2	8	
Dist. epi.	4				2	
Tibia						9
Prox. epi.						
Shaft	29	3	4	1	15	
Dist. epi.	5	2	1	3	3	

	NISP	TM	PM	CM	NISP with good preservation	MNE
Metatarsal						7
Prox. epi.	8	1		1	3	
Shaft	11		1	1	4	
Dist. epi.	2				1	
Carpal/tarsal	12				5	12
Phalanges	3				1	3
Other	1				1	1
Indeterminate	53	3	1	1	15	
Total	379	18	17	19	224	95

Table 4. Skeletal part profiles of large (sizes 4–6) carcasses at BK4b. NISP, number of identified specimens; TM, tooth marked specimens; PM, hammerstone-percussed specimens; CM, cut marked specimens; MNE, Minimum number of elements.

	NISP	TM	PM	CM	NISP with good preservation	MNE
Horn	11				11	2
Skull	26			1	18	3
Mandible	3				2	3
Teeth	44				39	
Vertebrae	17				7	10
Ribs	45	3	1	2	21	6
Scapulae	5				4	4
Pelves	7					2
Humerus						8
Prox. epi.	1					
Shaft	24	1	4	2	10	
Dist. epi.	1				1	
Complete	2				1	
Radius–ulna						4
Prox. epi.	5				2	
Shaft	5		1	1	2	
Dist. epi.	1				1	
Metacarpal						5
Prox. epi.	1				1	
Shaft	3				1	
Dist. epi.	5					
Femur						5
Prox. epi.	1				1	
Shaft	12		2	1	5	
Dist. epi.						
Tibia						8
Prox. epi.	1					
Shaft	41		9	6	15	
Dist. epi.	3			1	2	
Metatarsal						4
Prox. epi.	4				1	
Shaft	3		2		2	
Dist. epi.						
Carpal/tarsal	7				5	7

	NISP	TM	PM	CM	NISP with good preservation	MNE
Phalanges	5			1	4	5
Other	2				1	2
Indeterminate	127	4	3	1	35	
Total	412	8	22	16	192	78

When using indicators that potentially avoid the bias introduced by preferential deletion of cancellous bones by intervening biotic or physical post-depositional processes, long bones are evenly represented regardless of carcass size. The evenness index for small carcasses (0.98), medium-sized carcasses (0.96) and large carcasses (0.96) indicates that the dense elements comprising the high-survival skeletal set are well represented in the assemblage. This supports the interpretation that most carcasses were not selectively transported to the site, either because transport was of a shorter distance or because most carcasses were acquired at or very near the site.

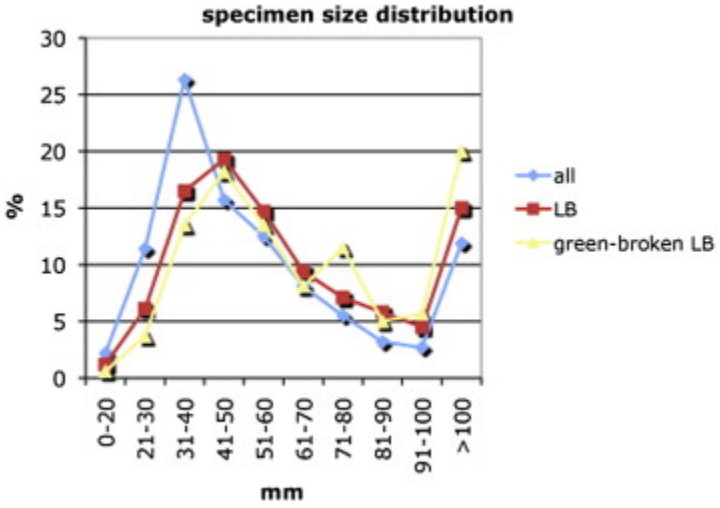

Fig. 10. Distribution of frequencies of bone specimens from BK4b, divided according to complete sample, only long bones and only green-broken long bones. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The low overall representation of axial elements suggests intense carnivore ravaging and/or the removal by sedimentary processes (e.g., hydraulic flows) of low density, easily transported elements. Voorhies's (1969) transport group one (axial and compact bones), for example, is underrepresented in the BK4b assemblage. When considering the size distribution of all specimens the only notable bias is the underrepresentation of bone fragments smaller than 20 mm (although a substantial amount of fragments <20 mm were retrieved in the sieved sediment). Specimens between 21 and 40 mm are the most abundant, and frequencies decrease until specimens larger than 100 mm are reached, most of which are represented by bone fragments from large carcasses. The pattern is slightly different for long bone fragments only. In this case, although specimens <50 mm are well represented, there is a clear underrepresentation of specimens <30 mm. This pattern is echoed in the sample of green-broken long bone specimens (Fig. 10). This could be due to either biotic (e.g., carnivore bone breaking) or physical (e.g., hydraulic jumbles) processes. However, if hydraulic processes were responsible for the low representation of smaller bone specimens, one would expect to see some spatially patterned

distribution of specimens according to their size (see below). Regardless, the low frequency of very small specimens does indicate at least a moderate level of post-depositional disturbance but does not refute its largely autochthonous nature.

4.2.2. Bone breakage

A total of 897 bone specimens could be identified as bearing green or/and dry breakage. Of these, 417 specimens showed green breakage and 480 had dry breakage. Most of the dry breakage was observed on long bones (n = 369), with the remainder documented on axial bones (n = 35), crania (n = 7), and compact elements (n = 6). Dry breakage documented in higher numbers on axial bones (n = 97), and more marginally on cranial (n = 25) and compact (n = 5) bones. However, most of them (n = 373) were documented on long bones or indeterminate fragments, regardless of carcass size.

A total of only 18 notches were identified, possibly because the extreme thickness of the dominant megafaunal remains lend themselves to the creation of spiral fractures rather than notches when broken when fresh. Most of the notches were either single or incomplete. The fact that notches appear on larger carcasses precludes a confident attribution of the breakage agent based on notch morphology (De Juana and Domínguez-Rodrigo, 2011). However, the type and frequency of surface modifications in the BK4b assemblage (see below) suggests that hammerstone-aided percussion was the main process of long bone fragmentation.

With the exception of a few elements that were preserved complete (Table 1, Table 2, Table 3), most long bones from all carcass sizes show green fractures. This is especially noticeable among megafaunal long bones where, for example, all the long bones from *Pelorovis*, *Sivatherium*, and other similarly-sized carcasses were broken while fresh (Fig. 11). The presence of impact flakes (Fig. 12) among carcasses of all sizes supports the contention that dynamic, hammerstone loading is largely responsible for the fragmentation of the appendicular elements. This is even observable on the few preserved elephant remains (Fig. 13).

The ratio of preserved shaft fragments (>20 mm) to limb bone MNE at BK4b is lower than that seen among modern experimental hammerstone-broken assemblages (Table 5). This is likely due, at least in part, to the underrepresentation of shaft fragments between 2 and 5 cm (see above), which in turn was probably caused by water disturbance. However, this only reflects a comparison between BK4b and experimental ratios across all elements. If NISP:MNE ratios are considered by element, the BK4b assemblage falls within the range of variation for every element of the hammerstone experimental set (Fig. 14). Furthermore, correlation varies according to carcass size. Due to the very small sample size, the original sets were multiplied by three before applying Spearman's correlation test; this does not affect the value of rho but modifies the value of probability. For small carcasses, a spearman correlation yielded a low positive and non-significant correlation (rho = 0.31, p = 0.316). In contrast, for medium-sized (rho = 0.94, p = 0.000) and large (rho = 1, p = 0.000) carcasses the correlation was strong and significant. This shows that the preservation of shafts per element is correlated to the type of bone as experimentally modeled. This further supports that post-depositional disturbance must have been low or moderate but not high. If such disturbance affected the assemblage, it must have biased the small (<5 cm) specimens, and the fragments of small-sized carcasses. The subset

comprising the bones from medium-sized and large carcasses seem to have kept a higher resolution.

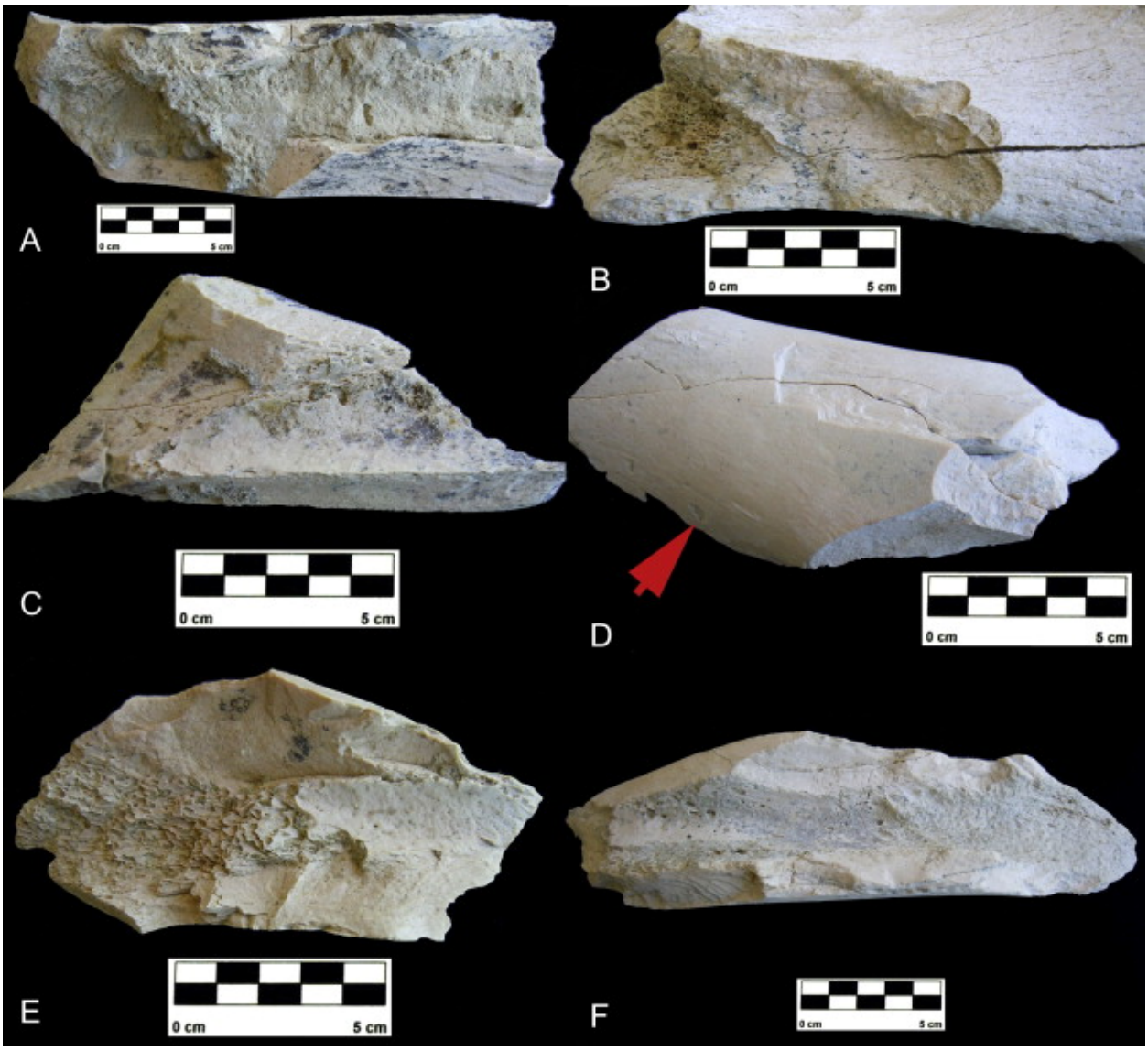

Fig. 11. Examples of green-broken long bones from size 4 to 5 carcasses (probably, *Sivatherium* and *Pelorovis-Synceros*) at BK4b. A, tibia shaft (BK 2984); B, radius shaft (BK 5205); C, femur shaft (BK 3106); D, humerus shaft (BK 4768) (arrow shows percussion mark); E, tibia shaft (BK 6957); F, tibia shaft (BK 5315).

Fig. 12. Examples of impact flakes from medium-sized and large carcasses. From upper left clockwise: BK 3209, BK 6119, BK 4395, BK 4201. Arrows show the bulbous ventral side.

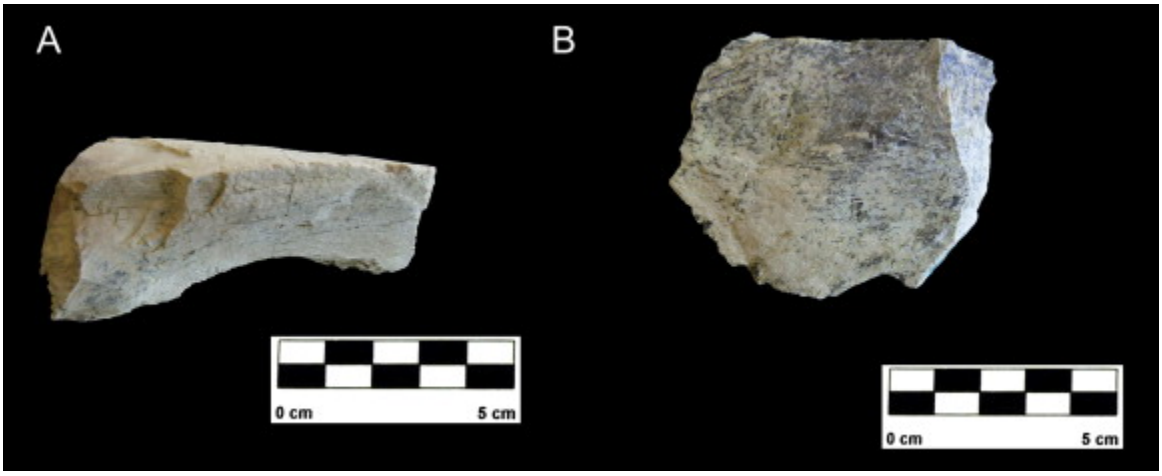

Fig. 13. A, example of impact flake from a proboscidean long bone shaft (BK; 2962). B, Impact flake from a proboscidean long bone shaft (BK 4641).

Table 5. Distribution of MNE and shaft fragments (>2 cm) of the main broken marrow-bearing bones according to carcass size at BK4b and some experiments with hammerstone bone breaking.

Carcass size						
	MNE	**BK4b**	**NISP per MNE**	**MNE**	**Experimental sample[a]**	
		Shaft NISP			**NISP per MNE**	**Range**
Small						
Humerus	2	3	1.5	8	9	(4–17)
Radius	1	1	1	8	11	(5–18)
Femur	1	1	1	8	9.2	(3–16)
Tibia	1	7	7	8	12.1	(7–19)
Medium-sized						
Humerus	7	30	4.2	8	11	(5–20)
Radius	4	8	2	8	7.8	(2–16)
Femur	4	10	2.5	8	7.8	(3–14)

Carcass size						
	MNE	BK4b	NISP per MNE	MNE	Experimental sample[a]	
		Shaft NISP			NISP per MNE	Range
Tibia	9	29	3.2	4	9.2	(6–13)
Large						
Humerus	6	24	4	8	7	(2–20)
Radius	4	5	1.3	4	4	(2–6)
Femur	5	12	2.4	5	5	(1–7)
Tibia	8	41	5.1	–	–	–

[a] Original data from the experimental set by Galán et al. (2009) for cow and goat bones, as a proxy for small and large carcasses and from De Juana and Domínguez-Rodrigo (2011) from equids as an analog for medium-sized carcasses.

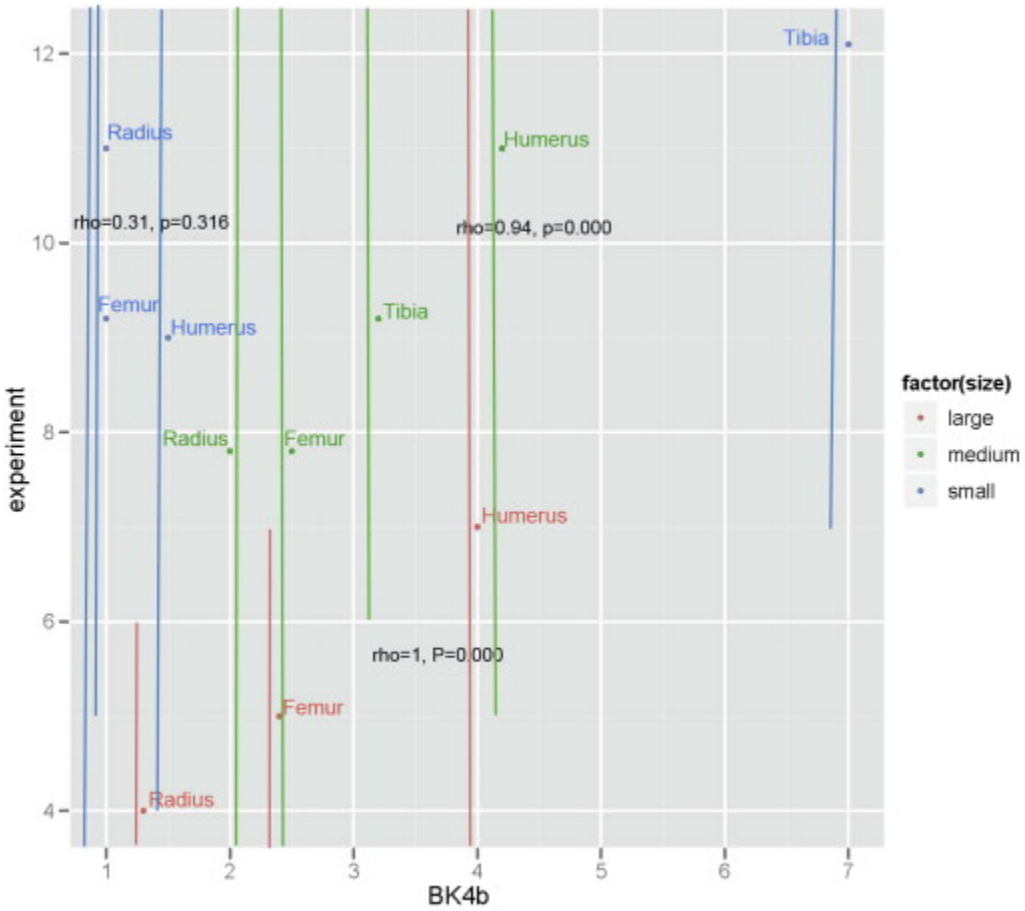

Fig. 14. NISP:MNE correlation (method = Spearman) per element between BK4b and experimental sets according to carcass size. Vertical bars show the range of variation for each bone in the experimental assemblage (se Table 4). Due to the very small sample size, the original sets were multiplied by three before applying Spearman's correlation test.

4.2.3. Bone surface modifications

Unfortunately, the BK4b bone surfaces are frequently poorly preserved, with about 52% (NISP = 457) of the sample exhibiting well-preserved cortical surfaces. The remainder of the sample is variously affected by soil chemical modifications caused by the presence of water or

prolonged exposure to humidity (4.5%; NISP = 53), biochemical modifications caused by fungi and bacteria (4.6%; NISP = 54), cortical weathering caused by abrasion or polishing of the surface by water (16%; NISP = 186), or by other unidentified processes. The similarity of subaerial weathering to diagenetic cortical modifications induced by soil geochemical conditions prevented confident identification of this surface modification in many instances. Nevertheless, subaerial weathering was evaluated on a sample of 384 specimens in which cortical modification could be confidently attributed to this process. Most of the well-preserved cortical surfaces (76%; NISP = 293) show no sign of weathering (stage 0) (Behrensmeyer, 1978). Weathering stage 1 has been documented on 14% (NISP = 54) of the sample, stage 2 on 5.7% (NISP = 22), stage 3 on 2.8% (NISP = 11) of the sample. Severe stages of 4 or higher were only documented on 1% (NISP = 4) of the assemblage.

Trampling was observed on 13% (NISP = 150) of the total assemblage, but is found in a substantially higher frequency (32.8%) among the well-preserved part of the assemblage. Microabrasion on cortical surfaces, which suggests friction of bone on the sedimentary matrix, was documented on 21.6% (NISP = 99) of specimens. This, together with the reported frequency of trampling, indicates that sediment macro- and micro-abrasion played an important role in the modification of bone surfaces, which in turn renders the identification of other marks (namely, cut marks) more challenging.

Carnivore damage in the form of tooth marks was documented on a small part of the assemblage (Table 2, Table 3, Table 4). Considering only the well-preserved part of the assemblage, tooth marks are preserved on 10% of bones from small animals (NISP = 4), 8% of bones from medium-sized animals (NISP = 18), and 4% (NISP = 8) of large animals. Tooth marks on long bone shafts are documented on 2 specimens out of a total of 29 (6.8%) small carcass shaft fragments, 7 out of 117 (5.9%) medium carcass shaft fragments, and 1 out of 143 (0.1%) large carcass shaft fragments. These frequencies are somewhat biased because they are based on a sample that includes both dry- and green-broken bones. Before comparing tooth mark percentages to analogical modern samples made up of only green-broken bone fragments, it is therefore necessary to correct for the bias introduced by dry breakage and poor cortical preservation in the BK assemblage.

Nine of the well-preserved shaft fragments from small carcasses show dry breakage, and the corrected estimate for tooth marks on shafts with good cortical preservation and green breakage is 8.3% (24 specimens). Twenty five well-preserved shaft specimens from medium-sized carcasses possess dry breakage, which yields a corrected percentage of tooth-marked shaft fragments of 6.7%. Twenty of the well-preserved shaft fragments from large carcasses show dry breakage, resulting in a corrected estimate for tooth marks on shafts with good cortical preservation and green breakage of 0.01% (133 specimens). Such low frequencies of tooth-marked long bone shafts are similar to experiments modeling the secondary access to hammerstone broken bones by durophagous carnivores (Blumenschine, 1995).

Percussion marks are more abundant than tooth marks, indicating the primary role of hominins in bone breaking. If using the well-preserved sample corrected for dry breakage, the percussion mark percentage for small carcasses is 8.3% (two percussed shaft fragments out of a sample of 24). Medium-sized carcasses show 12.5% of specimens with at least one percussion mark

(NISP = 13), while large carcasses show 15.7% of their shaft sample bearing a minimum of one percussion mark (NISP = 21). These frequencies are similar to those reported in hammerstone-broken experiments (Blumenschine, 1995), suggesting that most marrow exploitation at BK4b was carried out by hominins.

The sample of cut-marked bones from small animals is too small for meaningful behavioral analysis (NISP = 3), but cut-marked bones are relatively abundant on larger carcasses. A total of 19 medium-sized carcass specimens show cut marks and, using the well-preserved sample corrected for dry breakage, about 58% of cut-marked long bones occur on shafts. Femora (18%) are more frequently cut-marked than humeri (11.7%), and tibiae (22.2%) are more frequently than radii (14.2%). Only two metapodial specimens were found to preserve cut marks. Cut-marked specimens are also present on large carcasses, although they are fewer in number (NISP = 16). However, all but one of the cut-marked long bone specimens represent the shafts of meat-bearing bones (e.g., Fig. 15). Femora (16.6%) are cut-marked as frequently as humeri (16.6%), and tibiae (41.1%) are cut-marked more frequently than radii (20%). Cut marks are also documented on the axial skeleton (ribs and vertebrae) of both medium- and large-sized carcasses. The presence of cut marks on the ventral side of ribs shows that hominins were in some cases eviscerating carcasses at BK4b.

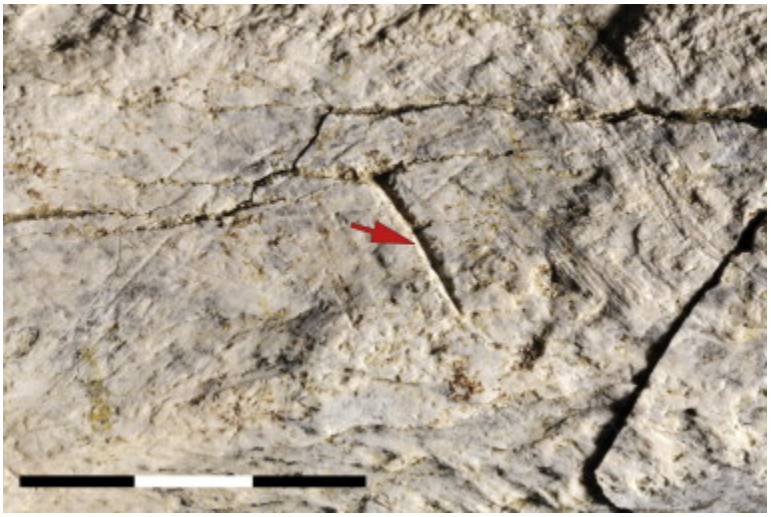

Fig. 15. Cut mark on the midshaft of a femoral fragment from a size-5 carcass (probably *Sivatherium*).

When analyzing cut marks, percussion marks, and tooth marks together, the results support early access by hominins to fleshed carcasses. A MXDA of experimental scenarios produced a two dimension solution that explained 92.49% of sample variance (factor 1 accounted for 77.33% of the variance) (Domínguez-Rodrigo et al., 2013c). Dimension 1 was determined by two variables: cut mark frequencies on shafts and cut mark frequencies on all bone parts, which clearly separated experimental sets (Fig. 16). Tooth mark frequencies were found to have the least impact on factor 1 (Fig. 16), although they did account for most variance in factor 2 (only 3% of total sample variance). Percussion marks are also a relevant contributor to the two dimension solution. Tooth marks are the least discriminatory of all the classes of bone surface modifications, which is not surprising given that primary access by felids to bones can generate

tooth mark frequencies similar to those seen when scavenging carnivores have access to hominin-discarded bones (Domínguez-Rodrigo et al., 2007).

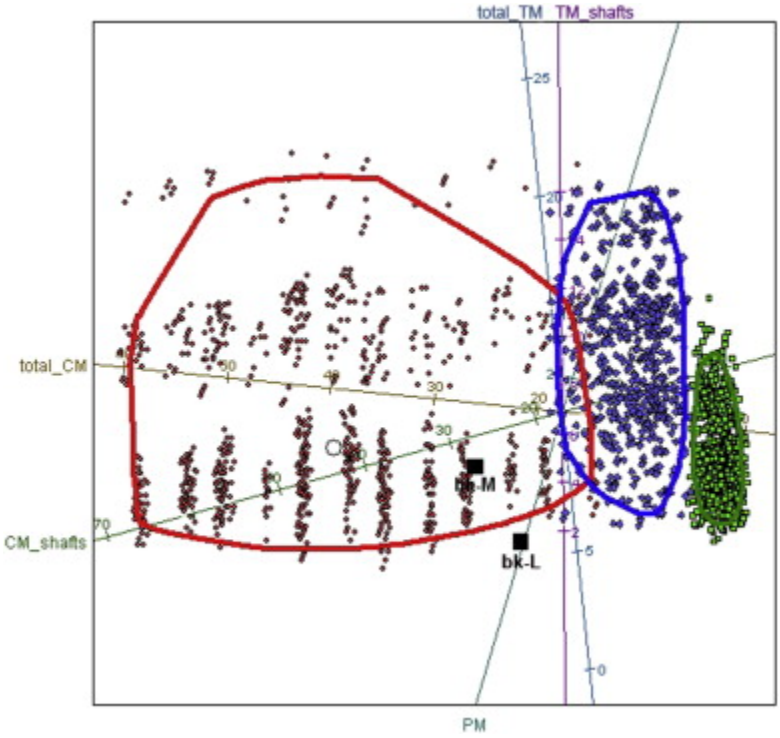

Fig. 16. Multiple discriminant analysis (using a canonical variate approach) on a bootstrapped sample of experimental sets: primary access to completely fleshed carcasses butchered with stone tools reproducing the H–C model (large red alpha bag to the left), secondary access to variously defleshed carcasses in the F–H–H model (medium-sized blue alpha bag), and secondary access to defleshed carcasses from the F–H model (small green alpha bag to the right). Centroid location within each alpha bag is also shown (squares). Cut marks appear as the most discriminant variables. Notice how the location of the BK medium-sized assemblage represents an assemblage of carcasses butchered by hominins after having primary access to them and where bulk defleshing instead of intensive flesh scrap removal was targeted. Data from Domínguez-Rodrigo et al. (2014c).

When the BK data were interpolated in the MXDA test, the BK4b medium-sized assemblage plots within the 95% confidence alpha bag of the H–C model, which suggests primary access to fleshed carcasses. Although the BK large-sized sample plots outside the alpha bags (probably because the experiments used to construct the MXDA were conducted on medium-sized carcasses), its location in proximity to the primary access alpha bag of the H–C model suggests that these carcasses were also substantially fleshed when butchered (Gidna et al., 2014).

4.3. Spatial analysis of taphonomic variables

The G function shows that the distribution of material at BK4b is generally isotropic with a significant degree of local clustering. The width of the envelopes shows limited variability of the null hypothesis (i.e., complete spatial randomness) and the scale of interaction (Fig. 17). A Fisher–Jenks selection of fragment size class intervals and their spatial distribution

(Figs. 18 and 19) shows that all specimens, regardless of size, are similarly represented in the excavated area. A variogram targeting an ellipsoid range of orientations (Fig. 19) also shows that no relationship exists between specimen size and spatial distribution. These findings call into question the assertion that the fluvial channel, while situated only a few meters away from where the assemblage was recovered, significantly altered the original spatial properties of the assemblage. If the fluvial processes that actually entombed the assemblage operated with substantial energy, a large part of the smallest fragments would have been removed and a redistribution of specimen sizes following the direction of flow (as seen in lag deposits) would have occurred. The presence of polished bones may indicate just such a process, and missing specimens <20 mm may also have been carried away by water. However, the high frequency of specimens between 30 mm and 50 mm indicates that hypothetical water transport would have been rather moderate. This can be tested through an examination of the correlation between specimen size distribution and the presence of polishing. If polishing resulted from bones being transported from elsewhere, the hydraulic flow responsible would have been selective in terms of transported specimen sizes. Spatial regression analysis shows no correlation of specimen size and polishing/abrasion; that is, polished and abraded bone is equally documented in all size categories (Fig. 20). This suggests that rather than arriving on site from elsewhere, polished bones more likely resulted from *in situ* chemical and physical modification, probably due to the slow abrasion of water circulation within the sedimentary matrix (Thompson et al., 2011). Further support for this interpretation comes from the observation that the spatial distribution of carbonate crusting of bone (indicative of humidity) overlaps with that of polished bones (Fig. 21). The overlap in the spatial distribution of bones with good and poor preservation also suggests differential modification due to the interaction of bone and soil properties (Fig. 22). Therefore, the overall impression is that water may have rearranged the original assemblage and, in doing so, probably transported away the smallest (<20 mm) specimens, but the energy of the process was not strong enough to transport away larger bones or to rearrange the remaining assemblage in any way that may have distorted its original spatial properties. The presence of several refits supports this contention (Fig. 23). The taphonomic and spatial analysis of the faunal assemblage of BK4b suggests that despite synsedimentary disturbance, the nature of the assemblage is autochthonous, with only limited rearranging.

Biostratinomic agents do not appear to show any preferential use of space at BK. Carnivores and trampling agents overlapped in the use of space (Fig. 19) while hominins, as the main agent of bone breakage (see above), also used the space isotropically (Figs. 22 and 24).

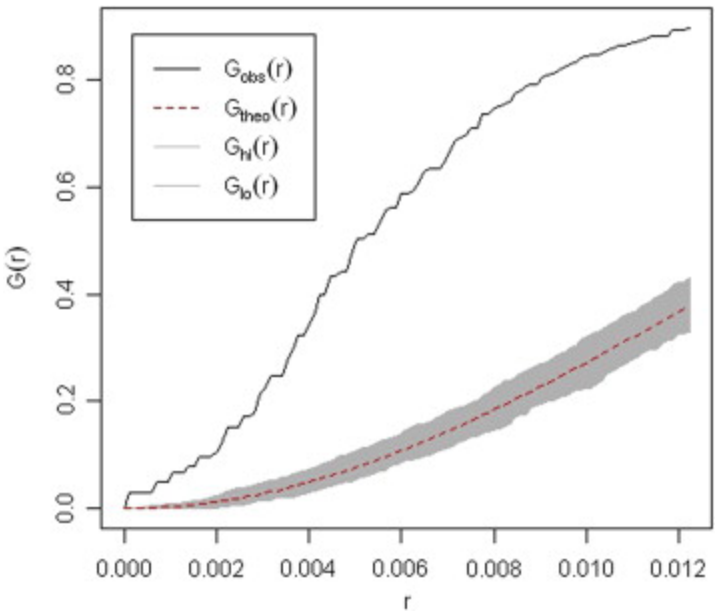

Fig. 17. Envelopes (grey) and observed values of the G function for the point pattern at BK4b.

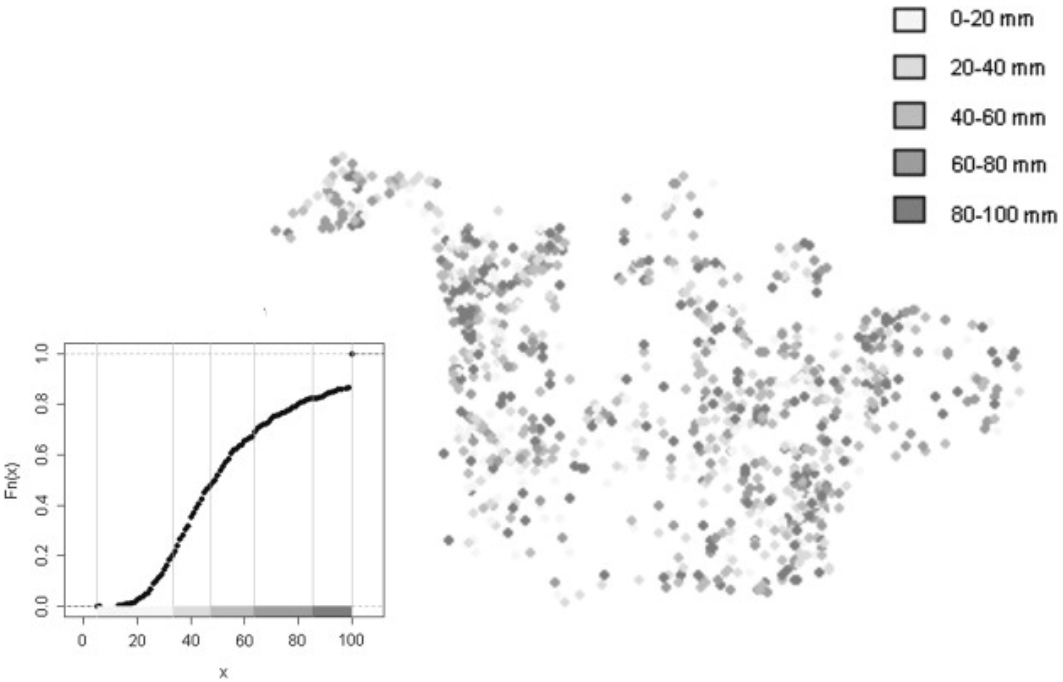

Fig. 18. Fisher–Jenks class distribution test according to specimen size (left). Plotting of each of the five classes of sizes determined by the Fisher–Jenks test, showing homogeneous distribution of all size classes (right).

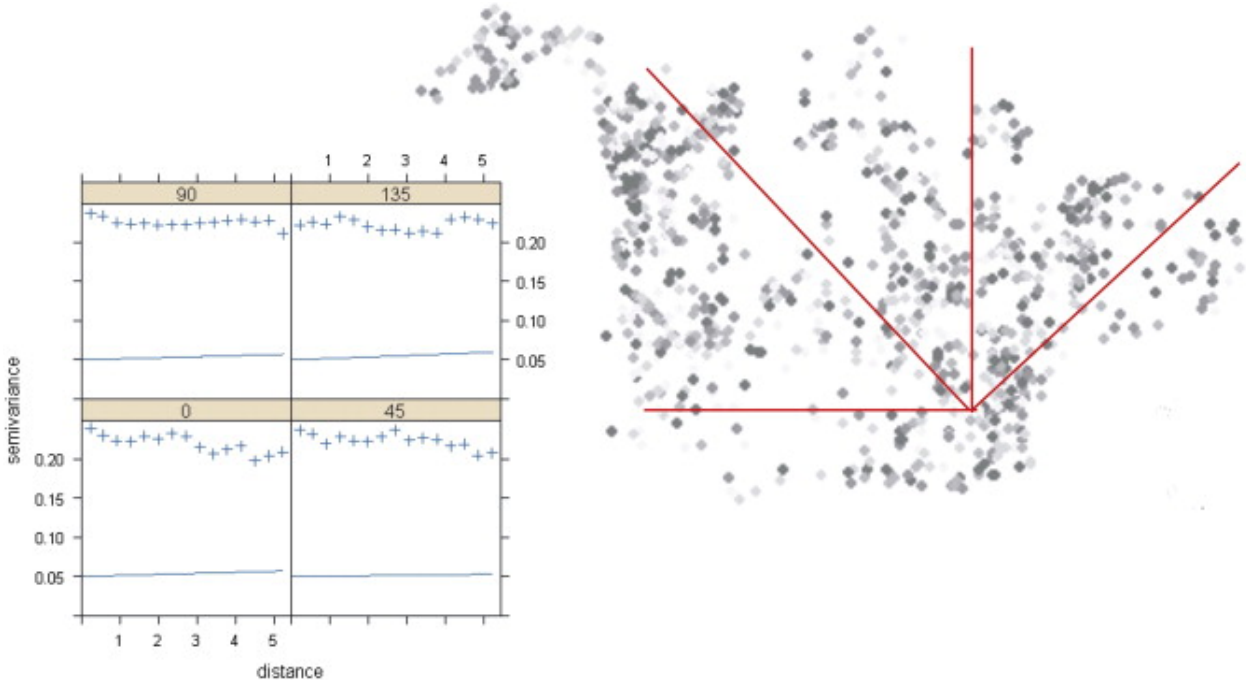

Fig. 19. Left, Variogram showing lack of relationship in specimen size distribution and distance from the southeastern corner of the area excavated (in four different orientations). Right, Sections of each of the orientations upon which the variogram is based.

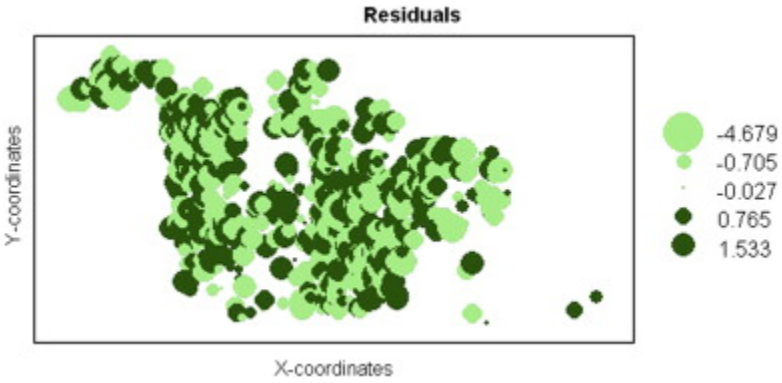

Fig. 20. Standardized residuals obtained in a linear regression model resulting from plotting the residuals of polished bone and specimen size against their spatial coordinates. Light-colored circles are negative residuals and darker circles are positive residuals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

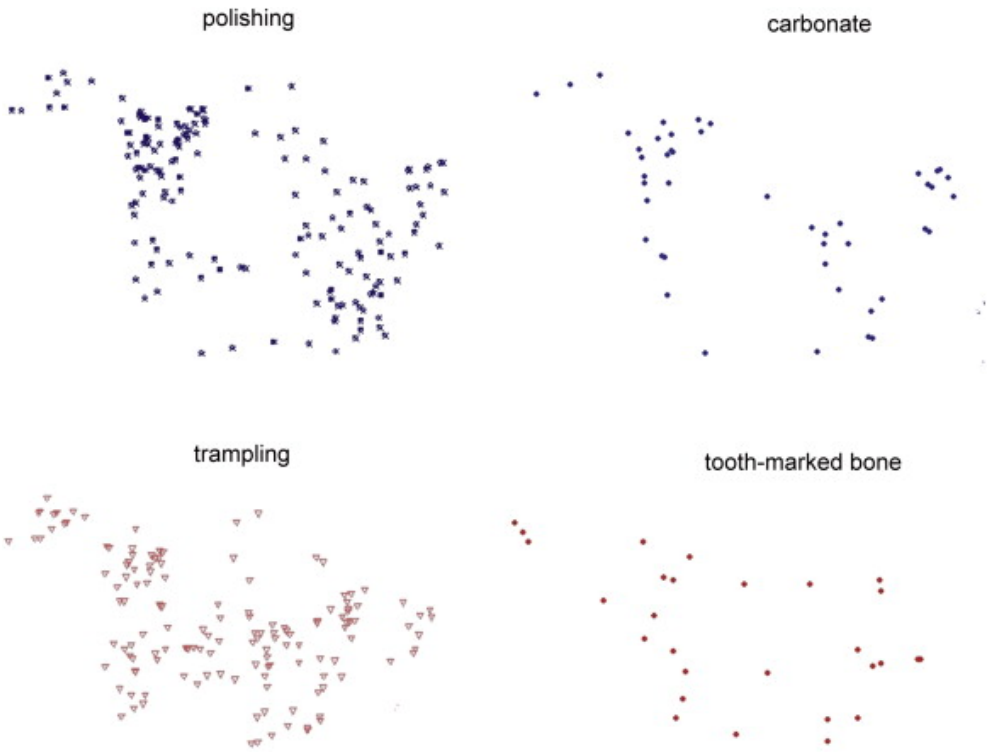

Fig. 21. Spatial distribution of faunal specimens from BK4b. All the plotted images show the spatial distribution of each bone specimen according to taphonomic variables: polished/abraded bone, bones with carbonate, trampling and tooth-marked specimens.

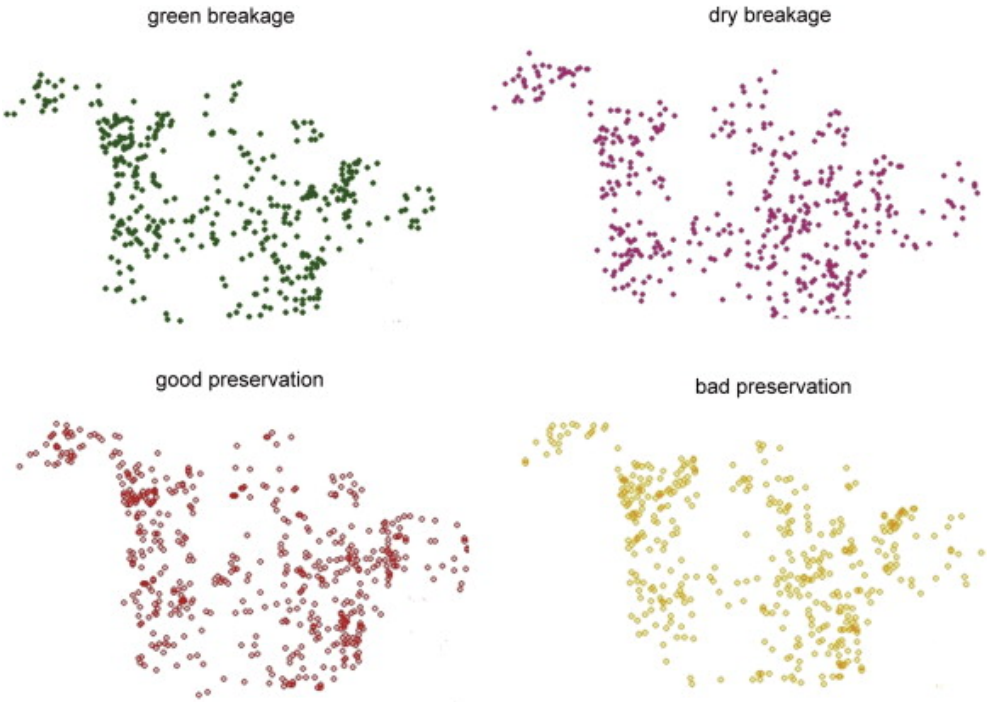

Fig. 22. Spatial distribution of the BK4b faunal specimens according to the following taphonomic variables: green breakage, dry breakage, good preservation and bad preservation.

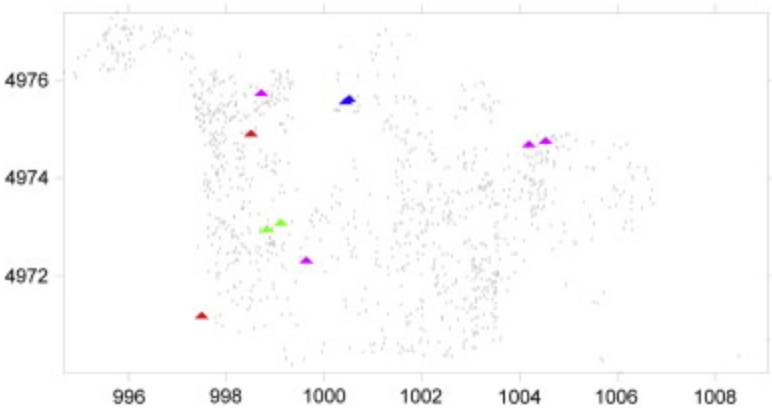

Fig. 23. Bone refits (same color icons) at BK4b.

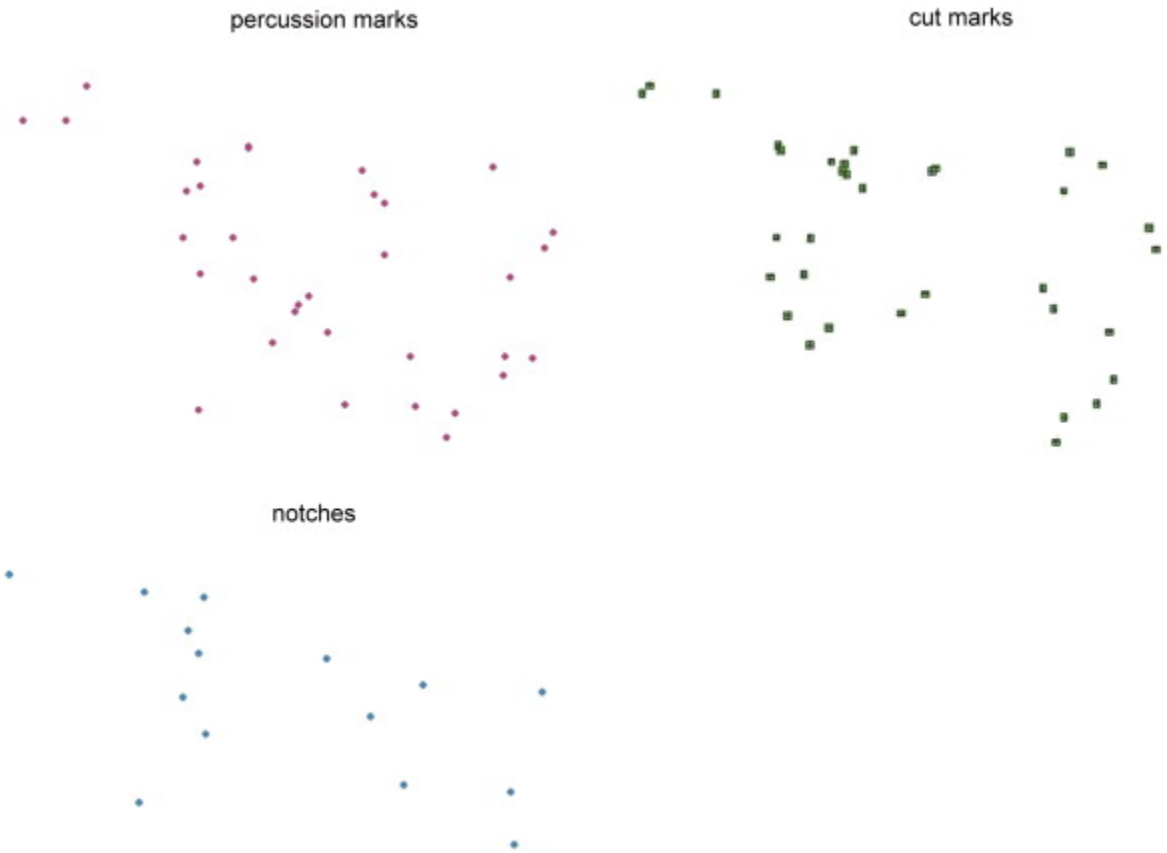

Fig. 24. Spatial distribution of the BK4b faunal specimens according to the following taphonomic variables: percussion marks, cut marks and percussion notches.

5. Discussion

Hominins at BK seem to have had access to large quantities of meat including, not insignificantly, from megafauna (Domínguez-Rodrigo et al., 2009). In fact, the amount of meat that hominins exploited at BK level 4b surpasses the evidence documented from other early Pleistocene sites, including the more ancient FLK *Zinj* site (Domínguez-Rodrigo et al., 2010b). This raises the important issue of the role that meat played in the adaptations and ecology of early Pleistocene humans.

5.1. Meat-eating as nutritional advantage or cost signaling?

Those that consider meat as a cost signaling product emphasize its marginal nutritional/energy return and its value as a social commodity (e.g., Hawkes, 1991, Hawkes, 2000, Hawkes et al., 1997, Lupo and O'Connell, 2002, Speth, 2010). While meat no doubt carries value above and beyond its nutritional yield, hunting among modern hunter–gatherers has been depicted as an inefficient way of getting food because it requires great amounts of time investment relative to its caloric return. Hadza men, for example, fail to kill on 97% of hunting days (Hawkes et al., 1997) and they may devote 4h/day to hunting, which yields a net benefit of 0.12 kg of meat per hour (Hawkes, 2000). This results in about a pound of meat per day. While this may at first glance seem marginal, such an amount of meat in not trivial: it can provide a large part of the daily nutritional requirements for a small nuclear family while, at the same time, keeping protein consumption within the healthy limits of less than 200 g/person/day. Apart from this, however, is the fact that the whole concept of inefficiency is erroneously based on the ratio of cal/h when it should be based on the net energy yield, in this case calories invested/calories returned. A Hadza hunter may certainly spend more time obtaining meat than others invest in gathering plants; however, the energy invested in gathering plants can be energetically demanding. For instance, tuber collecting by Hadza women requires 2–3 h on average of intensive effort that may include the removal of boulders, the sharpening of digging sticks, and nearly continuous digging. The amount of energy invested during the process is greater than that invested by the Hadza hunter who patiently waits behind a blind for game to get close enough to shoot (Marlowe, 2010). Even when a hunter actively searches for prey, the several hour walk (the Hadza do not generally run during foraging expeditions; Marlowe, 2010) may have required less energy than the effort of collecting certain plants and transporting them in heavy loads back to the camp. The point is that until researchers collect detailed data on the net energetic investment/returns of foragers, it is difficult to assess what strategy (hunting or plant gathering) is more efficient. Efficiency must also be considered not only at the individual level (the energy spent by the hunter in procuring the game) but on the return it provides to all the individuals (most of which invested no energy in obtaining it) who benefit from its procurement. Until these issues are more fully explored, it will be difficult to properly evaluate the role that meat plays in the diets of foragers and how this compares to other food items.

The solitary hunting model that characterizes some of these modern foragers may also be a recent acquisition enabled only by the use of bows and arrows as hunting weapons. This specialized projectile technology furnishes hunters with an independence that invites competition and increases the efficacy of cost signaling. The more collective hunting techniques that probably dominated for much of human evolution may have reduced competition among individuals that had to work together to ensure a successful outcome. This in turn probably minimized opportunities for individual cost signaling.

If the main impetus for hunting among modern foragers was cost signaling, one would expect meat to be preferentially distributed among non-kin rather than within nuclear families (Hawkes, 1991, Hawkes, 2000, Hawkes et al., 1997, Hawkes et al., 2001). Well controlled data on Hadza hunting and meat distribution shows just the opposite pattern. The amount of meat the hunter's nuclear family receives can be up to 40% of the prey (several times more than the rest of the

group members) and they typically keep the best parts of the prey (Wood and Marlowe, 2013). This supports the idea that the essential role of meat is as a nutritional resource rather than a social-promoting one.

Speth (2010) has recently cast doubt on the nutritional value of meat and argues instead that meat poisoning and its high specific dynamic action (the cost of metabolizing protein) renders meat a less than ideal dietary item. Health hazards due to protein overconsumption, which originate from the release of nitrogen and synthesis of ammoniac urea, become prevalent when meat constitutes more than 20–30% of the diet.

Meat constitutes 27% (in kg) or 19% (kca/day) of the food consumed by the Hadza (Marlowe, 2010). !Kung men contribute 20% more calories than women, and the bulk of these calories are from meat (Howell, 2010). In neither case does meat constitute more than 30% of the energy consumed by the group. Therefore, none of the risks described by Speth (2010) apply to most modern hunter–gatherers.

Viewed another way, protein can become toxic if more than 200 g per day are consumed. Given that 100 g of meat contain about 20 g of protein, the negative effect of meat would result only if daily meat consumption rose above 1000 g. No hunter–gatherer has been documented to exceed this quantity on a regular basis, and Speth (2010) acknowledges that San foragers consume a daily average of 230 g of meat (48.3 g of protein), which is well below any hazardous boundary. Hadza foragers consume a slightly smaller amount (Marlowe, 2010, Wood and Marlowe, 2013). Therefore, meat consumption among modern hunter–gatherers is normally well below the level of protein poisoning. This probably explains why the Hadza have been observed to hunt only one large animal a month (Lupo and O'Connell, 2002; although this varies seasonally, Wood and Marlowe, 2013).

Speth (2010) also argues that heavy meat consumption during certain times of the year produced weight loss among the San and Hadza. Marlowe (2010) shows that this assertion is incorrect regarding the Hadza, but in the case of the San, weight loss may be a temporary effect resulting from the body's readjustment to high protein intake. The body usually takes a few days to modify the enzymes involved in protein metabolism, after which a full recovery is made (Speth, 2010). Therefore, while Speth (2010) argues that too much protein may lead to death, the lethal amount is rarely, if ever, reached as the body readapts to high protein consumption in 2–3 weeks. This purported lethal amount is well above the threshold of protein intake in modern foragers. It thus seems that modern foragers are typically able to enjoy the benefits of meat while avoiding the risks.

The high specific dynamic action of metabolizing protein can be balanced with a slightly higher intake of meat, a situation that is even more important for the consumption of plant protein. Proteins can be divided into high quality and low quality, depending on the following factors:

1. Biological value (BV). This depends on the fraction on nitrogen retained by the organism

$$\mathrm{BV} = (\mathrm{RN}/\mathrm{AN}) \times 100$$

where RN is Retained Nitrogen and AN is Absorbed Nitrogen.

2. Digestibility (D). This is defined as the percentage of consumed nitrogen that does not appear in the feces:

$$D = (AN/CN) \times 100$$

where CN is Consumed Nitrogen

3. Amino acid scoring (Aa S). The standard requirement of essential amino acids (E Aa) is determined as follows:

$$\text{Aa S} = (\text{mg EAa/g of Test Protein})/(\text{mg EAa/g of Reference Protein})$$

When combining these three factors, high quality, or complete, proteins are defined as those that are digested, absorbed, and retained in high quantities and provide all the essential amino acids in the right doses. Meat and animal products provide the highest degree of all of these factors. Plant proteins are less easily digested and retained by the body and, thus, require increased quantities (Vázquez et al., 2005). For example, 100 g of meat contain about 20 g of protein with a BV of 75%, while 100 g of soy may contain 35 g of protein, but with a BV of only 60%, requires the processing of more food. Plant proteins also do not usually contain all the essential amino acids and require combinations of different plants to fulfill them. In addition, plants such as cereals and legumes, which have high protein and amino acid content, are typically not available in African savannas. Speth (2010) correctly describes the virtues of mongongo nuts for the Ju/'hoansi, with its high levels of fat, protein, and essential amino acids. However, this nutritious resource is only available for short periods each year. How do the Ju/'hoansi fulfill their protein requirements when this fruit is unavailable? The G/wi use Tsin beans and marula nuts, which are high in protein and fat also contain all the essential amino acids. These also are only available part of the year. None of these plants can provide a year-round supply of the quality and type of protein required by humans. Furthermore, they lack some of the conditionally essential amino acids (e.g., proline, serine, arginine, tyrosine, glycine glutamine), some of which are crucial during pregnancy.

Meat is the only source that can provide a year-round supply of protein in the amounts and types necessary for humans living in an African savanna. Meat also possesses docosahexaenoic acid (DHA) and fat, both of which are necessary for human metabolism (Speth, 2010). Meat is an excellent source of essential vitamins like A and B12 that are not found in mongongo and amarula nuts, legumes, or baobab fruits. Plants with vitamin A appear not to exist in Hadza land, and yet the Hadza do not suffer from vitamin A deficiency because they obtain it from meat (Marlowe, 2010). An advantage of obtaining vitamin A from meat instead of plants is that vitamin A in meat is found as the preformed vitamin retinol, which can be directly and efficiently absorbed by the organism (between 70 and 90%). Vitamin A in plants is found in the form of carotenoid pigments, which are less efficiently absorbed by the organism (20–25%) (Vázquez et al., 2005).

It could be argued that insects were a viable alternative source of vitamin B12 for early hominins. Certain insects, including some species of termites, do contain vitamin B12 that is produced by their gut bacteria, but many other species contain low levels or no vitamin B12 (Wakayama et al., 1984). Hadza encounter many termites in their territory but have not been observed eating them (Marlowe, 2010). Meat also contains phosphorous, which is more easily absorbed than the phosphorous present in cereals and legumes because, in the latter, it is found as phytic acid, which must be hydrolyzed before absorption.

To sum up: animal food in African savannas provides a large amount of complete, highly digestible protein that contains a diversity of essential and conditionally essential amino acids, a large amount of fat (including the highly valuable DHA), and a wealth of micronutrients that are essential for human metabolism (iron, easy to absorb phosphorous, zinc, selenium, and vitamins A and B12). No single plant product contains all of these nutrients. Nor can one find plants that provide a year-round source of nutrients in the high doses per unit weight that meat does. In order to approach the nutritional value of meat, a combination of different plants would need to be obtained and ingested in higher frequencies, all of which would entail a higher energetic cost through additional metabolic processing. If African savannas contained plant products containing all the nutrients of meat (which they do not), hominins may still have selected meat because it would enable them to enjoy all the caloric and nutritional benefits of a food that was faster to process. If hominins were under selective pressure to reduce the digestive tract to fuel a large brain without modifying basal metabolic energy (Aiello and Wheeler, 1995), then the adoption of regular meat-eating seems to be a probable response. This appears to have been exactly what groups of lower Pleistocene hominins at sites like BK and, even earlier, at FLK Zinj (Domínguez-Rodrigo et al., 2009a, Domínguez-Rodrigo et al., 2010b) did. One question still remains: could the human brain have evolved without meat-eating?

Speth (2010) claims that big game hunting was a very inefficient and unreliable way of putting food on the table. We, on the other hand, argue that it was the only way in which a diet with the nutritional demands of human metabolism could have emerged in an African savanna. Meat is only unreliable in the sense that it does not contribute to human diets on a daily basis, but it does contribute 20–30% of the yearly energetic needs of modern African foragers and provides essential nutrients (like vitamin B12) very difficult to obtain otherwise.

5.2. Meat bonanza at BK and its adaptive meaning

The distribution of cut marks, percussion marks, and tooth marks on the bone assemblage from BK4b demonstrates that hominins enjoyed early access to medium-sized carcasses and, most probably, to fleshed megafaunal carcasses. The presence of cut marks on meat-bearing long bones (e.g., humerus, femur, and tibia), axial bones (ribs), and cranial (mandible) elements shows that defleshing of megafauna (including both *Pelorovis* and *Sivatherium*) occurred repeatedly at the same place. This is supported by the abundant evidence of marrow exploitation by hominins in the form of percussion marks and green fractures on all appendicular elements. Although BK4b does not contain the abundance of megafaunal individuals reported previously by Gentry (1967), this unit has yielded remains from elephant, hippopotamus, rhinoceros, *Pelorovis* (two individuals) and *Sivatherium* (two individuals). Elements from hippopotamus and rhinoceros are very scarce, and therefore little can be said of their depositional history. The

presence of pelvic and cranial remains from hippopotami is suggestive of autochthonous deposition. Likewise, the presence of bones from most of the anatomical regions of what is most likely a single *Sivatherium* (skull, vertebrae, ribs, pelvis, and most long bones, including compact elements) individual indicates that hominins exploited at least one individual that died at or near the spot where it was butchered (Fig. 25).

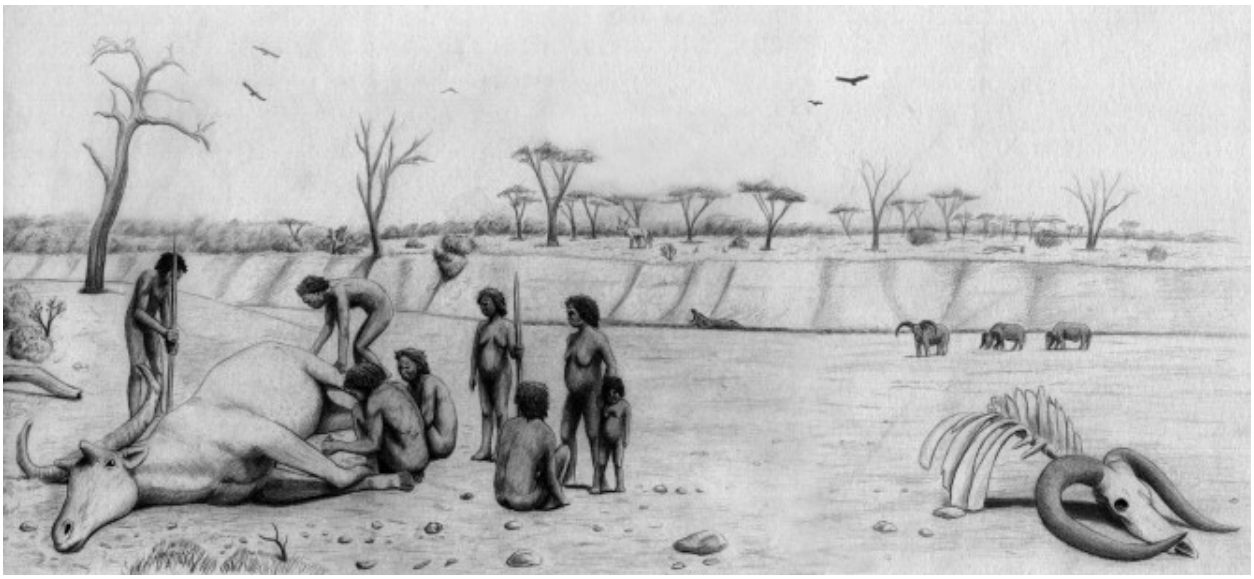

Fig. 25. Reconstruction of the deposition and hominin butchery of one Sivatherium at BK4b. Remains of Pelorovis can also be seen (author: M. Ansón).

In situ death of megafaunal individuals does not seem to have been an uncommon occurrence in the BK area, as the axial and appendicular parts of an elephant carcass within the overlying BK3b sediments is also indicative of an autochthonous deposition. The presence of a partial *Pelorovis* carcass (including cranial, axial, and limb elements) found by Leakey at BK within the so-called "*Pelorovis* level", also suggests that natural deaths may have resulted in the deposition of some carcasses, especially since the long bones of that particular individual were complete and bore no hominin-imparted modifications.

BK4b (like the rest of the BK deposit) is a time-averaged assemblage. The fluvial depositional setting where the site was formed and the low degree of subaerial weathering on bones suggest relatively active sedimentation and an attenuated exposure time. Despite this, the time interval between sedimentary processes must have been sufficiently prolonged to allow multiple, time-averaged depositional episodes of faunal accumulation, each with their own taphonomic history. This would explain the paucity of elements from some taxa (e.g., hippopotamus) and the unevenness in the skeletal representation of other taxa (e.g., one *Sivatherium* individual represented by a partial carcass and another by just a mandible). Deposition within some of the sedimentary sequences must have involved water disturbances. As with BK4b, the clay matrix within which artifacts and fossils are embedded is suggestive of a low energy depositional environment. It could be argued that if the particle source was devoid of detritic materials, a clay could still reflect a relatively high energy depositional context; however, the presence of sand and gravel both under and above BK4b is rather indicative of low to moderate energy during sedimentation. The presence of a small part of sand particles within the clay stratum also

indicates that water flowed with enough energy to deposit clay and sand. The latter is probably responsible for the abundant abrasion experienced by the BK fauna. Abundant evidence for tramped bone also attests to the fact that the BK area was a focal point on the landscape for mammals during the formation of the deposit.

The rarity of axial bones from small and medium-sized carcasses could be due to either selective transport by hominins, or post-depositional deletion by carnivores and hydraulic transport. However, if one examines the absolute frequency of axial bones, it could be argued that some of medium-sized carcasses are in fact represented by axial anatomical parts, which may suggest either complete carcass transport or initial deposition and subsequent butchery at the site.

It is possible that BK4b simply represents a butchery site where megafauna redundantly died and hominins and carnivores sequentially exploited them. This interpretation would contradict the original representation of the site as a mass killing locus (Leakey, 1954). However, the hundreds of kilograms of lithic raw material introduced by hominins to the site far exceed what would be needed to produce the tools for butchering the animals represented. This could suggest, tentatively, that BK4b was used for hominin activities besides butchery. The study of the lithic materials should shed more light on this issue.

BK4b presents a curious depositional combination in which faunal materials show an even scattering whereas lithic materials show several distinct clusters of nodular artifacts (Fig. 5; see also Supplementary information for 3D reconstructions and map of the site). This multi-cluster pattern contrasts with the single dense cluster of fossils and tools at FLK Zinj and could be suggestive of some sort of differentiated use of space. For example, two areas at BK4b in which large-sized anvils (one of them showing percussion damage) are surrounded by green-broken bone fragments appear to have been used specifically for bone-breaking. The western half of the site also contains a higher amount of nodular artifacts, whereas flakes seem more abundant on the eastern half, where a large part of a *Sivatherium* carcass was concentrated, suggesting some functional association.

All these spatial interpretations of BK4b must remain preliminary at this point, as a larger area needs to be exposed to better document any heterogeneity in spatial distribution. The area exposed also needs to be excavated into the underlying stratigraphic sequence to further understand the nature of the deposit. A small test trench (1 × 1 m) showed that dense concentrations of materials in a sandy context underlie BK4b, perhaps indicating a higher influence of post-depositional disturbance by water. It also shows that vertical boundaries will need to be established beyond the different lithological nature of both geological layers to determine if BK4b does represent a discrete horizon or a more vertically dispersed deposit. The latter situation will probably require a redefinition of the archaeological level and a requantification of its faunal contents. Because such effort will require several more years (work in progress), we felt it was important to present a complete faunal analysis of the BK4b material excavated to date in order to address the issue of meat eating by early Pleistocene hominins. If one accepts that a large part of the megafauna exploited at BK4b might have been dead upon their encounter by hominins, the redundant acquisition of meat in this way may have voided any benefit accrued by signaling since no hominin individual could have claimed responsibility for obtaining the carcass. The fact that hominins seem to have repeatedly and systematically

exploited all resources from these large animals could also indicate a real need for the nutritional benefits of meat. Hominin groups at that time may also have been larger, and processing large animals would have conferred energetic advantage to the entire group. Small groups of just a few individuals would render the thorough butchery of a *Sivatherium* or *Pelorovis* individual unnecessary. Perhaps most importantly, further paleoecological information must be gathered to understand the ecological circumstances that encouraged the formation of an extremely dense concentration of fauna (especially megafauna) at this particular location.

6. Conclusions

A moderate part of a paleosurface unearthed at BK4b (see Supplementary information for an interactive 3D reconstruction of three different areas) showed that a large amount of stone tools and bones from macro- and megafauna deposited on this paleosurface are functionally related. Butchery was repeatedly performed on a wide range of animals spanning different sizes, from gazelle to elephant. Therefore, BK4b must have acted as a magnet for hominins and other carnivores to exploit a diversity of fauna, which frequented the spot, probably due to the presence of water. However, there are abundant fluvial channels associated with the uppermost section of Bed II in other areas of the gorge, such as RHC near the paleolake, or PLK and only scanty evidence of hominin presence exist in those fluvial settings. The dense concentration of animals concentrated at BK is undocumented in any other part of the gorge. Therefore, other reasons must exist for the presence of such a high biomass in that locus. Future research must target this enigmatic question. The immediate surrounding of BK seems to have been a fairly dry area, since the carbonate eroded by the BK river system shows karstification and dissolution. The "caliche" surface of the carbonate would not have been apt for dense vegetation. The ecological information retrieved from the animal taxa represented at the site indicates an overall open landscape, as indicated by the dominance of grazers and open-habitat faunas (alcelaphini, antilopini, and equids). However, the presence of water dependent reduncini and browsers (tragelaphini and Giraffidae) indicates local fauna and the presence of bush/tree vegetation, probably in the immediate vicinity of the site.

The amount of meat consumed at BK4b, as indicated by the number and size of individuals butchered, is far greater than that documented at FLK Zinj or any other early Pleistocene site. This emphasizes that meat eating was a crucial factor in early hominin adaptation, which suggests that its consumption was more likely the end product of a physiological need for adaptive purposes rather than a cost signaling byproduct. This interpretation is reinforced by the dominance of megafaunal remains at the site. This suggests that their deposition was autochthonous and, therefore, that even if they were systematically exploited by hominins, the null hypothesis is that they were scavenged, in the absence of indicators of megafauna predation by hominins. Cost signaling has been argued to be prompted by hunting but not necessarily scavenging (Speth, 2010). The exploitation of other different and probably allochthonous taxa shows that hominins may have expanded the use of the site beyond a mere butchery spot. The hundreds of kg of raw material imported into the site is suggestive of BK4b having functioned as a multi-activity place. Future work should determine the site functionality through its diverse occupations, and provide more information to support a social interpretation thereof. Despite being time-averaged, the clay stratum where BK4b is embedded indicates a short sedimentary process. Such a dense and spatially extended archaeological level is suggestive of a large

hominin group. It could be argued that at the end of the Pleistocene, human groups may have become bigger than in previous times and this may have been reflected in higher amounts of raw material accumulated at sites (per each discrete horizon) and in a more thorough defleshing and demarrowing of megafaunal remains, which would have been unlikely in the event of a small group of hominins processing such a large carcass type. Future research at the site should build on these preliminary interpretations.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quaint.2013.08.015.

References

Aiello, L., Wheeler, P., 1995. The expensive tissue hypothesis. The brain and the digestive system in human and primate evolution. Current Anthropology 36, 199–221.

Alcalá, L., 1994. Macromamíferos neógenos de la fosa Alfambra-Teruel. Instituto de Estudios Turolenses, Zaragoza.

Barba, R., Domínguez-Rodrigo, M., 2005. The taphonomic relevance of the analysis of bovid long limb bone shaft features and their application to element identification: study of bone thickness and morphology of the medullary cavity. Journal of Taphonomy 3, 17–42.

Behrensmeyer, A.K., 1978. Taphonomic and ecologic information from bone weathering. Paleobiology 4, 150–162.

Bivand, R., Pebesma, E.J., Gómez-Rubio, V., 2009. Applied Spatial Data Analysis with R. Springer, New York.

Blumenschine, R.J., Selvaggio, M.M., 1988. Percussion marks on bone surfaces as a new diagnostic of hominin behavior. Nature 333, 763–765.

Blumenschine, R.J., Selvaggio, M.M., 1991. On the marks of marrow bone processing by hammerstones and hyenas: their anatomical patterning and archaeological implications. In: Clark, J.D. (Ed.), Cultural Beginnings: Approaches to Understanding Early Hominin Life Ways in the African Savanna. R. Habelt. Bonn, GMBH, pp. 17–32.

Blumenschine, R.J., 1988. An experimental model of the timing of hominin and carnivore influence on archaeological bone assemblages. Journal of Archaeological Science 15, 483–502.

Blumenschine, R.J., 1995. Percussion marks, tooth marks and the experimental determinations of the timing of hominin and carnivore access to long bones at FLK Zinjanthropus, Olduvai Gorge, Tanzania. Journal of Human Evolution 29, 21–51.

Bunn, H.T., 1981. Archaeological evidence for meat-eating by Plio-Pleistocene hominins from Koobi Fora, Kenya. Nature 291, 574–577.

Bunn, H.T., 1982. Meat-eating and Human Evolution: Studies on the Diet and Subsistence Patterns of Plio-pleistocene Hominins in East Africa (Ph. dissertation). University of California, Berkeley.

Bunn, H.T., 1994. Early Pleistocene hominin foraging strategies along the ancestral Omo River at Koobi Fora, Kenya. Journal of Human Evolution 27, 247–266.

Bunn, H.T., 1997. The bone assemblages from the excavated sites. In: Isaac, G.Ll (Ed.), Koobi Fora Project Monograph, vol. 5. Clarendon Press, Oxford, pp. 402–458.

Capaldo, S.D., Blumenschine, R.J., 1994. A quantitative diagnosis of notches made by hammerstone percussion and carnivore gnawing in bovid long bones. American Antiquity 59, 724–748.

Capaldo, S.D., 1997. Experimental determinations of carcass processing by Plio-Pleistocene hominins and carnivores at FLK 22 (Zinjanthroprus), Olduvai Gorge, Tanzania. Journal of Human Evolution 33, 555–597.

Capaldo, S.D., 1998. Methods, marks and models for inferring hominin and carnivore behaviour. Journal of Human Evolution 35, 323–326.

Carbone, C., Teacher, A., Rowcliffe, J.M., 2007. The costs of carnivory. PLoS Biology 5 (2), e22. http://dx.doi.org/10.1371/journal.pbio.0050022.

Cleghorn, N., Marean, C.W., 2004. Distinguishing selective transport and in situ attrition: a critical review of analytical approaches. Journal of Taphonomy 2, 43–67.

Costamagno, S., 2002. Laboratory taphonomy-material loss and skeletal part profiles: the example of Saint Germain la Rivière (Gironda, France). Archaeometry 44 (3), 495–509.

Creel, S., Creel, N.M., 1995. Communal hunting and pack size in African wild dogs, Lycaon pictus. Animal Behaviour 50, 1325–1339.

De Juana, S., Domínguez-Rodrigo, M., 2011. Testing analogical taphonomic signatures in bone breaking: a comparison between hammerstone-broken equid and bovid bones. Archaeometry 53, 996–1011.

de la Torre, I., Benito-Calvo, A., 2013. Application of GIS methods to retrieve orientation patterns from imagery: a case study from Beds I and II, Olduvai Gorge. Journal of Archaeological Science 40, 2446–2457.

Delpeche, F., Villa, P., 1993. Activités de chasse et boucherie dans la grotte des Eglises. In: Desse, J., Audoin-Rouzeau, F. (Eds.), Exploitation des animaux sauvages a travers le Temps. IV, Colloque International de l'Homme et l'Animal. Editions APDCA, pp. 79–102.

Diez-Martín, F., Sánchez Yustos, P., Dominguez-Rodrigo, M., Mabulla, A.Z.P., Barba, R., 2009. Where Olduvai hominins making butchering tools or battering tools? Analysis of a recently excavated lithic assemblage from BK (Bed II, Olduvai Gorge, Tanzania). Journal of Anthropological Archaeology 28, 274–289.

Domínguez-Rodrigo, M., Barba, R., Egeland, C.P., 2007. Deconstructing Olduvai. Springer, New York.

Domínguez-Rodrigo, M., Barba, R., 2006. New estimates of tooth marks and percussion marks from FLK Zinj, Olduvai Gorge (Tanzania): the carnivore-hominin-carnivore hypothesis falsified. Journal of Human Evolution 50, 170–194.

Domínguez-Rodrigo, M., Martínez-Navarro, B., 2012. Taphonomic analysis of the early Pleistocene (2.4 Ma) faunal assemblage from AL894 (Hadar, Ethiopia). Journal of Human Evolution 62, 315–327.

Domínguez-Rodrigo, M., Mabulla, A., Bunn, H.T., Barba, R., Diez-Martin, F., Egeland, C.P., Espilez, E., Egeland, A., Yravedra, J., Sánchez, P., 2009a. Unraveling hominin behavior at another anthropogenic site from Olduvai Gorge (Tanzania): new archaeological and taphonomic research at BK, Upper Bed II. Journal of Human Evolution 57, 260–283.

Domínguez Rodrigo, M., Alcalá, L., Luque, L., 2009b. Peninj: a Research Project on the Archaeology of Human Origins (1995e2005). Oxbow, Harvard, Massachusetts.

Domínguez-Rodrigo, M., Mabulla, A.Z.P., Bunn, H.T., Diez-Martin, F., Baquedano, E., Barboni, D., Barba, R., Domínguez-Solera, S., Sanchez, P., Ashley, G.M., Yravedra, J., 2010a. Disentangling hominin and carnivore activities near a spring at FLK North (Olduvai Gorge, Tanzania). Quaternary Research 74, 363–375.

Domínguez-Rodrigo, M., Bunn, H.T., Mabulla, A., Ashley, G.M., Diez-Martín, F., Prendergast, M.E., Yravedra, J., Sánchez, A., Baquedano, E., 2010b. New excavations at the FLK Zinjanthropus site and its surrounding landscape and their behavioral interpretations. Quaternary Research 74, 315–332.

Domínguez-Rodrigo, M., Diez-Martín, F., Barba, R., Yravedra, J., Bunn, H.T., Mabulla, A., Baquedano, E., Uribelarrea, D., 2014a. A taphonomic study of the faunal assemblage of the main site at SHK (Bed II, Olduvai Gorge, Tanzania). Quaternary International 322-323, 153–166.

Domínguez-Rodrigo, M., Pickering, T.R., Mabulla, A.Z.P., Musiba, C., Bunn, H.T., Baquedano, E., Diez-Martin, F., Sánchez, P., Santonja, M., Uribelarrea, D., Pérez-González, A., Barba, R., Yravedra, J., Barboni, D., Gidna, A., Heaton, J., 2014b. The first associated partial skeleton of a Paranthropus boisei from BK (Bed II, Olduvai Gorge, Tanzania). PLOS One submitted for publication).

Domínguez-Rodrigo, M., Bunn, H.T., Yravedra, J., 2014c. A critical re-evaluation of bone surface modification models for inferring fossil hominin and carnivore interactions through a multivariate approach: application to the FLK Zinj archaeofaunal assemblage (Olduvai Gorge; Tanzania).

Domínguez-Rodrigo, M., 1997. Meat eating by early hominids at FLK Zinj 22 site, Olduvai Gorge, Tanzania: an experimental approach using cut-mark data. Journal of Human Evolution 33, 669–690.

Egeland, C.P., Domínguez-Rodrigo, M., 2008. Taphonomic perspectives on hominid site use and foraging strategies during Bed II times at Olduvai Gorge, Tanzania. Journal of Human Evolution 55, 1031–1052.

Faith, J.T., Gordon, A.D., 2007. Skeletal element abundances in archaeofaunal assemblages: economic utility, sample size, and assessment of carcass transport strategies. Journal of Archaeological Science 34, 872–882.

Fiori, I., Bondoli, L., Coppa, A., Macchiarelli, R., Russom, R., Kashkay, H., Solomon, T., Rook, L., Libsekal, Y., 2004. Taphonomic analysis of the late early Pleistocene bone remains from Buia (Dandiero Basin, Danakil Depression, Eritrea): evidence for large mammal and reptile butchering. Rivista Italiana di Paleontologia e Stratigrafia 110, 89–97.

Fiorillo, A.R., 1991. Taphonomy and depositional setting of Careless Creek Quarry (Judith River formation), Wheatland County, Montana, U.S.A. Palaeogeography, Palaeoclimatology, Palaeoecology 81, 281–311.

Fisher, N.I., 1995. Statistical Analysis of Circular Data. Cambridge University Press, Cambridge.

Galán, A., Fernández, M., De Juana, S., Domínguez-Rodrigo, M., 2009. A new experimental study on percussion marks and notches and their bearing on the interpretation of hammerstone-broken faunal assemblages. Journal of Archaeological Science 36, 776–784.

Gentry, A.W., 1967. Pelorovis Oldowayensis, Reck, an Extinct Bovid from East Africa. Bulletin, British Museum of Natural History, p. 14 n. 7.

Gidna, A., Kisui, A.B., Domínguez-Rodrigo, M., 2014. An Ecological Neo-taphonomic Study of Carcass Consumption in Tarangire National Park (Tanzania) and its Relevance for Human Evolutionary Biology. Quaternary International 322-323, 167–180.

Gittleman, J.L., 1989. Carnivore group living: comparative trends. In: Gittleman, J.L. (Ed.), Carnivore Behavior, Ecology and Evolution. Cornell University Press, Ithaca, New York, pp. 183–207.

Hall, P., 1992. The Bootstrap and Edgeworth Expansion. Springer, New York.

Hastie, T.J., Tibshirani, R.J., 1996. Discriminant analysis by Gaussian mixtures. Journal of the Royal Statistical Society Series B 58, 158–176.

Hawkes, K., O'Connell, J.F., Blurton Jones, N.G., 1997. Hadza women's time allocation, offspring provisioning, and the evolution of long postmenopausal life spans. Current Anthropology 38 (4), 551–577.

Hawkes, K., O'Connell, J.F., Blurton Jones, N.G., 2001. Hadza meat sharing. Evolution and Human Behaviour 22 (2), 113–142.

Hawkes, K., 1991. Showing off: tests of an hypothesis about men's foraging goals. Ethology and Sociobiology 12, 29–54.

Hawkes, K., 2000. Hunting and the evolution of egalitarian societies: lessons from the Hadza. In: Diehl, M.W. (Ed.), Hierarchies in Action: Cui Bono? Occasional Paper 27. Southern Illinois University, Center for Archaeological Investigations, Carbondale, IL, pp. 59–83.

Hay, R., 1976. Geology of the Olduvai Gorge. University of California Press, Berkeley.

Howard, P., 2007. Archaeological Survey and Mapping. Taylor and Francis, London.

Howell, N., 2010. Life Histories of the Dobe !Kung: Food, Fatness and Well-being over the Life Span. California University Press, Los Angeles.

Kruuk, H., 1972. The Spotted Hyena: a Study of Predation and Social Behavior. University of Chicago Press, Chicago.

Leakey, L.S.B., 19th June 1954. The Giant Animals of Prehistoric Tanganyika and the Hunting Grounds of Chellean Man. New Discoveries in the Olduvai Gorge. Illustrated London News, pp. 1047–1051.

Leakey, M.D., 1971. Olduvai Gorge. In: Excavations in Bed I and II, 1960–1963, vol. 3. Cambridge University Press, Cambridge.

Leakey, L., 1994. Olduvai Gorge. Excavations in the Bed II, IV and Masek Beds. Cambridge University Press, Cambridge.

Lenoble, A., Bertran, P., 2004. Fabric of Paleolithic levels: method and implications for site formation processes. Journal of Archaeological Science 31, 457–469.

Lupo, K.D., O'Connell, J.F., 2002. Cut and tooth mark distributions on large animal bones: ethnoarchaeological data from the Hadza and their implications for current ideas about early human carnivory. Journal of Archaeological Science 29 (1), 85–109.

Lyman, R., 1994. Vertebrate Taphonomy. Cambridge University Press, Cambridge.

Ma, J., He, X., 2008. A fast fixed-point BYY harmony learning algorithm on Gaussian mixture with automated model selection. Pattern Recognition Letters 29, 701–711.

Marean, C.W., Kim, S., 1998. Mousterian large mammals from Kobech Cave. Current Anthropology 39, 79–113.

Marean, C.W., Cleghorn, N., 2003. Large mammal skeletal element transport. Applying foraging theory in a complex taphonomic system. Journal of Taphonomy 1, 15–42.

Marean, C.W., Frey, C.J., 1997. The animal bones from caves to cities: reverse utility curves as methodological artifacts. American Antiquity 62, 698–711.

Marean, C.W., Abe, Y., Nilssen, P., Stone, E., 2001. Estimating the Minimum Number of Skeletal Elements (MNE) in zooarchaeology: a review and a new image-analysis GIS approach. American Antiquity 66, 333–348.

Marean, C.W., Domínguez-Rodrigo, M., Pickering, T.R., 2004. Skeletal element equifinality in zooarchaeology begins with method: the evolution and status of the "shaft critique". Journal of Taphonomy 2, 69–98.

Marean, C.W., 1998. A critique of the evidence for scavenging by Neanderthals and early modern humans: new data from Kobeh Cave (Zagros Mountains, Iran), Die Kielders Cave 1 layer 10, South Africa. Journal of Human Evolution 35, 111–136.

Marlowe, F., 2010. The Hadza. Hunter Gatherers of Tanzania. California University Press, Los Angeles.

McPherron, S.J.P., 2005. Artifact orientations and site formation processes from total station proveniences. Journal of Archaeological Science 32, 1003–1014.

Monahan, C.M., 1996. New zooarchaeological data from Bed II, Olduvai Gorge, Tanzania: implications for hominid behavior in the Early Pleistocene. Journal of Human Evolution 31, 93–128.

Münzel, S.C., 1988. Quantitative analysis and archaeological site interpretation. Archaeozoologia 2, 93–110.

Pante, M.C., Blumenschine, R.J., Capaldo, S.D., Scott, R.S., 2012. Validation of bone surface modification models for inferring hominin and carnivore feeding interactions, with reapplication to FLK 22, Olduvai Gorge, Tanzania. Journal of Human Evolution 63, 395–407.

Patou-Mathis, M.E., 1984. Contribution a l'étude des mammifères des couches supérieures de la Grotte du Lazaret. M. A. Dissertation. Université de la Sorbonne, Paris (unpublished).

Patou-Mathis, M.E., 1985. La fracturation des os longs de grands mammifères: élaboration d'un lexique et d'une fiche type. Outillage peu élabore en os et en bois de cervidés. Artefacts 1, 11–22.

Pickering, T.R., Marean, C., Domínguez-Rodrigo, M., 2003. Importance of limb bone shaft fragments in zooarchaeology: a response to "On in situ attrition and vertebrate body part profiles" (2002), by M.C. Stiner. Journal of Archaeological Science 30, 1469–1482.

Pickering, T.R., Domínguez-Rodrigo, M., Egeland, C., Brain, C.K., 2004a. New data and ideas on the foraging behaviour of Early Stone Age hominins at Swartkrans Cave, South Africa. South African Journal of Science 100, 215–219.

Pickering, T.R., Domínguez-Rodrigo, M., Egeland, C., Brain, C.K., 2004b. Beyond leopards: tooth marks and the contribution of multiple carnivore taxa to the accumulation of the Swartkrans member 3 fossil assemblage. Journal of Human Evolution 46, 595–604.

Pickering, T.R., Egeland, C., Domínguez-Rodrigo, M., Brain, C.K., Schnell, A., 2008. Testing the "shift in the balance of power" hypothesis at Swartkrans, South Africa: hominin cave use and subsistence behavior in the Early Pleistocene. Journal of Anthropology and Archaeology 27, 30–45.

Sanhouni, M., Rosell, J., van der Made, J., Vergés, J., Ollé, A., Kandi, N., Harichane, Z., Derradji, A., Medig, M., 2013. The First Evidence of Cut Marks and Usewear Traces

from the Plio-Pleistocene Locality of El-Kherba (Ain Hanech), Algeria: Implications for Early Hominin Subsistence Activities Circa 1.8 Ma.

Selvaggio, M.M., 1994. Identifying the Timing and Sequence of Hominid and Carnivore Involvement with Plio-pleistocene Bone Assemblages from Carnivore Tooth Marks and Stone-tool Butchery Marks on Bone Surfaces (Unpublished Ph. D. dissertation). Rutgers University.

Selvaggio, M.M., 1998a. Concerning the three stage model of carcass processing at FLK Zinjanthropus: a reply to Capaldo. Journal of Human Evolution 35, 313–315.

Selvaggio, M.M., 1998b. Evidence for a three-stage sequence of hominid and carnivore involvement with long bones at FLK Zinjanthropus, Olduvai Gorge, Tanzania. Journal of Archaeological Science 25, 191–202.

Speth, J., 2010. The Paleoanthropology and Achaeology of Big Game Hunting. Protein, Fat or Politics? Springer, New York.

Thompson, C.E., Ball, S., Thompson, T.J.U., Gowland, R., 2011. The abrasion of modern and archaeological bones by mobile sediments: the importance of transport modes. Journal of Archaeological Science 38, 784–793.

Toots, H., 1965. Orientation and distribution of fossils as environmental indicators. In: Nineteenth Field Conference of the Wyoming Geological Association, pp. 219–229.

Vázquez, C., de Cos, A., López-Nomdedeu, C., 2005. ALimentación y nutrición. Diaz de Santos, Madrid.

Villa, P., Mahieu, E., 1991. Breakage patterns of human long bones. Journal of Human Evolution 21, 27–48.

Voorhies, M., 1969. Taphonomy and Population Dynamics of an Early Pliocene Vertebrate Fauna, Knox County, Nebraska. University of Wyoming, Laramie. Contributions to Geology Special Paper No. 1.

Wakayama, E.J., Dillwith, J.W., Howard, R.W., Blomquist, G.J., 1984. Vitamin B12 levels in selected insects. Insect Biochemistry 14, 175–179.

Wood, B., Marlowe, F., 2013. Household and kin provisioning by Hadza men. Human Nature (in press).

Woodcock, N.H., 1977. Specification of fabric shapes using an eigenvalue method. Geological Society of America Bulletin 88, 1231–1236.

Yravedra, J., Domínguez-Rodrigo, M., 2009. The shaft-based methodological approach to the quantification of long limb bones and its relevance to understanding hominin subsistence in the Pleistocene: application to four Paleolithic sites. Journal of Quaternary Science 24, 85–96.